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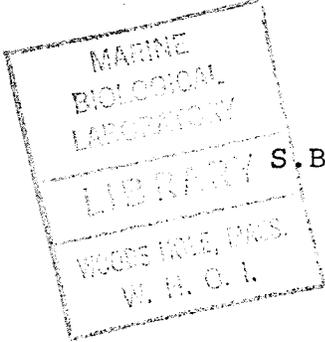
FUNCTIONAL ANATOMY OF  
THE MACROURIDAE  
(TELEOSTEI, GADIFORMES)

by

TRACY McLELLAN

S.B., Massachusetts Institute of  
Technology

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and

WOODS HOLE OCEANOGRAPHIC INSTITUTION

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Signature of Author.....

Department of Biology  
May 28, 1976

Certified by.....

Thesis Supervisor

Accepted by.....

Chairman, Joint Committee in Biological  
Oceanography  
Massachusetts Institute of Technology  
Woods Hole Oceanographic Institution

## ABSTRACT

## FUNCTIONAL ANATOMY OF THE MACROURIDAE (TELEOSTEI, GADIFORMES)

Tracy McLellan

Submitted to the Department of Biology on May 28, 1976 in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

Osteology and myology of the head of 21 species of macrourids and two closely related species are described. A general model of the mechanics of the macrourid head during feeding has been developed based on the anatomical findings. The structure of the head and integration of morphological units are used to explain specializations in the utilization of different food resources. Pelagic prey are the source of food for the most primitive species and for a few of the more specialized ones. A highly protrusible mouth and long rostrum are adaptations for benthic feeding and have appeared in three independent evolutionary lines within the group. Macrourids that are predators on benthos tend to be small and live at depths shallower than 2000 meters.

Thesis Supervisor: J. Frederick Grassle

Title: Associate Scientist

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## TABLE OF CONTENTS

<u>subheading</u>	<u>page</u>
TITLE PAGE	1
ABSTRACT	2
TABLE OF CONTENTS	3
ACKNOWLEDGEMENTS	5
BIOGRAPHICAL NOTE	7
LIST OF FIGURES	8
LIST OF TABLES	13
INTRODUCTION	14
I. Distribution of the Macrouridae	16
II. Trophic Ecology of the Macrouridae	18
III. Systematics of the Macrouridae	20
METHODS	24
MATERIALS	25
ANATOMICAL ABBREVIATIONS	29
GENERAL MODEL OF THE MACROURID HEAD	32
ANATOMY OF THE MACROURIDAE	67
I. Species Examined	68
II. Cranium	76
III. Infraorbital Series	146
IV. Suspensorium and Preopercle	165
V. Opercular Series	176
VI. Jaws: Premaxilla, Maxilla, and Mandible	177
VII. Hyoid Apparatus	215
VIII. Pharyngeal Jaws	215

<u>subheading</u>	<u>page</u>
IX. Muscles of the Head	215
A. Muscles Between Suspensorium and Jaws	215
B. Muscles Between the Cranium and Suspensorium	240
C. Muscles Between the Cranium and Opercle	241
D. Ventral Muscles of the Head	241
E. Epaxial Muscles	242
X. Ligaments	242
A. Intrinsic Ligaments of the Jaws	242
B. Other Ligaments of the Head	265
COMPARATIVE FUNCTIONAL MORPHOLOGY	267
I. Rostrum Architecture	267
II. Protrusibility of the Upper Jaw	273
III. Suspensorium and Hyoid	280
IV. Summary	283
FEEDING HABITS OF THE MACROURIDAE	284
DISCUSSION	294
I. Availability of Food	294
II. Predator Strategy and Morphological Adaptations for Creating Suction	299
SUMMARY	301
BIBLIOGRAPHY	305

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## BIOGRAPHICAL NOTE

Tracy McLellan was born on October 22, 1949, in Corning, New York, the daughter of Elizabeth Scoville and George William McLellan. She attended elementary school in Corning and secondary schools in Ithaca, New York. She graduated from Ithaca High School in 1966. After attending College Cevenol, France, for a year, she studied zoology for two years at McGill University, Montreal and transferred to the Massachusetts Institute of Technology in September 1969. She received an S.B. degree from M.I.T. in June 1971, and immediately became a graduate student in the M.I.T.-Woods Hole Oceanographic Institution Joint Program in Biological Oceanography.

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## LIST OF FIGURES

Figure	Page
1 Diagram of the mechanical units of the head with the mouth closed	34
2 Lateral view of the skull of <u>Macrourus berglax</u>	37
3 Premaxilla and maxilla of <u>Macrourus berglax</u>	39
4 Suspensorium of <u>Macrourus berglax</u>	41
5 Superficial cheek muscles of <u>Macrourus berglax</u>	46
6 Deep cheek muscles of <u>Mataeocephalus acipenserinus</u>	48
7 Ventral muscles of <u>Coelorinchus coelorinchus carminatus</u>	51
8 Pharyngeal muscles of <u>Coelorinchus occa</u>	54
9 <u>M. berglax</u> , sternohyoideus pulled back	57
10 <u>M. berglax</u> , epaxial muscles pulled back	59
11 <u>M. berglax</u> , primordial ligament pulled back	63
12 Diagram of the mechanical units of the head with the mouth open	65
13 Dorsal view of the skull of <u>Macruronus novaezelandiae</u>	78
14 Lateral view of the skull of <u>M. novaezelandiae</u>	80
15 Dorsal view of the skull of <u>Steindachneria argentea</u>	82
16 Lateral view of the skull of <u>S. argentea</u>	84
17 Dorsal view of the skull of <u>Bathygadus macrops</u>	86
18 Lateral view of the skull of <u>B. macrops</u>	88
19 Lateral view of the skull of <u>Lepidorhynchus denticulatus</u>	91
20 Dorsal view of the skull of <u>Malacocephalus occidentalis</u>	93
21 Lateral view of the skull of <u>M. occidentalis</u>	95

22	Dorsal view of the skull of <u>Nezumia bairdii</u>	97
23	Lateral view of the skull of <u>N. bairdii</u>	99
24	Dorsal view of the skull of <u>Mataeocephalus acipenserinus</u>	102
25	Lateral view of the skull of <u>M. acipenserinus</u>	104
26	Dorsal view of the skull of <u>Coryphaenoides rupestris</u>	106
27	Lateral view of the skull of <u>C. rupestris</u>	108
28	Dorsal view of the skull of <u>Coryphaenoides carapinus</u>	110
29	Lateral view of the skull of <u>C. carapinus</u>	112
30	Dorsal view of the skull of <u>Coryphaenoides armatus</u>	114
31	Lateral view of the skull of <u>C. armatus</u>	116
32	Dorsal view of the skull of <u>Coryphaenoides acrolepis</u>	118
33	Lateral view of the skull of <u>C. acrolepis</u>	120
34	Dorsal view of the skull of <u>Coryphaenoides leptolepis</u>	123
35	Lateral view of the skull of <u>C. leptolepis</u>	125
36	Lateral view of the skull of <u>Coryphaenoides pectoralis</u>	127
37	Dorsal view of the skull of <u>Macrourus berglax</u>	129
38	Dorsal view of the skull of <u>Abyssicola macrochir</u>	131
39	Lateral view of the skull of <u>A. macrochir</u>	133
40	Dorsal view of the skull of <u>Coelorinchus coelorinchus carminatus</u>	135
41	Lateral view of the skull of <u>C.c. carminatus</u>	137
42	Dorsal view of the skull of <u>Coelorinchus chilensis</u>	139
43	Lateral view of the skull of <u>C. chilensis</u>	141
44	Dorsal view of the skull of <u>Coelorinchus longissimus</u>	143
45	Lateral view of the skull of <u>C. longissimus</u>	145

		10
46	Dorsal view of the skull of <u>Coelorinchus occa</u>	148
47	Lateral view of the skull of <u>C. occa</u>	150
48	Dorsal view of the skull of <u>Coelorinchus jordani</u>	152
49	Lateral view of the skull of <u>C. jordani</u>	154
50	Dorsal view of the skull of <u>Coelorinchus innotabilis</u>	156
51	Lateral view of the skull of <u>C. innotabilis</u>	158
52	Lateral view of the skull of <u>Coelorinchus japonicus</u>	160
53	Dorsal view of the skull of <u>Trachyrincus helolepis</u>	167
54	Lateral view of the skull of <u>T. helolepis</u>	169
55	Superficial cheek muscles of <u>Macruronus novaezelandiae</u>	171
56	Superficial cheek muscles of <u>Steindachneria argentea</u>	179
57	Superficial cheek muscles of <u>Bathygadus macrops</u>	181
58	Superficial cheek muscles of <u>L. denticulatus</u>	184
59	Superficial cheek muscles of <u>M. occidentalis</u>	186
60	Superficial cheek muscles of <u>N. bairdii</u>	188
61	Superficial cheek muscles of <u>M. acipenserinus</u>	190
62	Superficial cheek muscles of <u>Coryphaenoides rupestris</u>	193
63	Superficial cheek muscles of <u>C. carapinus</u>	195
64	Superficial cheek muscles of <u>C. armatus</u>	197
65	Superficial cheek muscles of <u>C. pectoralis</u>	199
66	Superficial cheek muscles of <u>Abyssicola macrochir</u>	202
67	Superficial cheek muscles of <u>C.c. carminatus</u>	204
68	Superficial cheek muscles of <u>C. chilensis</u>	206
69	Superficial cheek muscles of <u>C. occa</u>	208
70	Superficial cheek muscles of <u>C. jordani</u>	210

		11
71	Superficial cheek muscles of <u>Coelorinchus innotabilis</u>	212
72	Superficial cheek muscles of <u>C. japonicus</u>	214
73	Superficial cheek muscles of <u>Trachyrincus helolepis</u>	217
74	Deep cheek muscles of <u>Macruronus novaezelandiae</u>	221
75	Deep cheek muscles of <u>Steindachneria argentea</u>	223
76	Deep cheek muscles of <u>Bathygadus macrops</u>	225
77	Deep cheek muscles of <u>Lepidorhynchus denticulatus</u>	227
78	Deep cheek muscles of <u>Malacocephalus occidentalis</u>	229
79	Deep cheek muscles of <u>Nezumia bairdii</u>	231
80	Deep cheek muscles of <u>Coryphaenoides armatus</u>	233
81	Deep cheek muscles of <u>Abyssicola macrochir</u>	235
82	Deep cheek muscles of <u>Coelorinchus occa</u>	237
83	Deep cheek muscles of <u>Trachyrincus helolepis</u>	239
84	Ventral muscles of <u>Bathygadus macrops</u>	244
85	Ventral muscles of <u>Malacocephalus occidentalis</u>	246
86	Ventral muscles of <u>Nezumia bairdii</u>	248
87	Ventral muscles of <u>Mataeocephalus acipenserinus</u>	250
88	Ventral muscles of <u>Coryphaenoides rupestris</u>	252
89	Ventral muscles of <u>Coryphaenoides armatus</u>	254
90	Ventral muscles of <u>Coryphaenoides acrolepis</u>	256
91	Ventral muscles of <u>Coryphaenoides leptolepis</u>	258
92	Ventral muscles of <u>Coelorinchus occa</u>	260
93	Ventral muscles of <u>Coelorinchus innotabilis</u>	262
94	Ventral muscles of <u>Trachyrincus helolepis</u>	264

		12
95	Dorsal view of the head of <u>Coelorinchus</u> <u>occa</u>	271
96	Lateral view of three species with the mouth open	275
97	Medial view of the premaxilla and maxilla	279
98	Ventral view of three species with the mouth open	282.

## LIST OF TABLES

Table 1	Stomach contents of macrourids	286
Table 2	Summary of the feeding habits of the species examined in relation to size, depth of occurrence, mouth size, length of the premaxilla, and rostrum length	303

## INTRODUCTION

Fishes of the family Macrouridae are the dominant component of the benthopelagic fauna of the deep sea. They show a number of unique morphological characteristics which have been used to unite them into a fairly well-defined group and which are presumably adaptations to the benthopelagic environment. There are several possible sources of food for animals that swim over the bottom, including benthic invertebrates, epibenthic animals and large pieces of detritus that have fallen to the bottom and midwater animals. This study is an attempt to understand the role of the benthopelagic fauna in benthic food chains through the examination of functional anatomy of the heads of the Macrouridae, which show adaptations to many of the possible sources of food on the bottom of the deep sea.

The head of a fish serves several functions. It is the bow of a streamlined body that moves through water and holds the organs of smell, sight, hearing, taste and most of the lateral sense organs. The gills are ventilated by movements of the gill covers and the mouth. The most striking differences between the heads of different kinds of fishes are related directly to feeding habits (Gregory, 1933).

The heads of teleosts are complex structures with

numerous joints and possibilities for movement. The function of several of the bones and muscles are the same throughout teleosts, while there is great variation in the morphology and in the function of some of the other components of the head. Functional analysis of morphological characters has been used in explaining the interdependency of the evolution of morphological characters in some groups of fishes (Liem, 1967, 1970, 1973).

The movements of the fish head have been investigated in a number of groups of fishes by examination of preserved or freshly killed specimens (Tchernavin, 1953; Alexander, 1966, 1967a, 1967b), by filming live fish (Nyberg, 197 ; Liem, 1967; Lauder, 1976), by surgically impairing ligaments (Liem, 1970; Lauder, 1976) and by measurement of muscle contraction by electromyography (Osse, 1969; Ballintijn, van den Burg and Egberink, 1972; Liem and Osse, 1975). Methods used depend in part on the ability to keep the fish in captivity. Deep sea fishes rarely show any signs of life after they have been trawled out of the ocean, so that a study of the mechanical workings of the head of fishes from great depth is limited to the examination of dead specimens. The work that has been done on live fishes serves as a basis on which to interpret the functions of the morphological characters found in other fishes that are not so convenient to work on. The morphology of the macrourids is so extreme in some ways that the functions show up more clearly than in more generalized fishes.

It is possible to study the functional morphology of the Macrouridae by examining the anatomy of the bones, muscles, connective tissue and joints of the head of several species of the family. A general model of the possible movements of the head is presented here that is based on those morphological characters which were found in all macrourids. Comparison of the differences between species will illuminate the morphological characters which are important in adaptations to the utilization of different types of food resources.

#### I. Distribution of the Macrouridae

The Macrouridae are the dominant fishes of the benthopelagic fauna - those animals that hover just off the bottom of the deep sea. There are more than 300 species in the family, more species than in any other family common in that environment (Okamura, 1970b; Marshall and Iwamoto, 1973). They have been found in all oceans of the world except the Arctic (Marshall and Iwamoto, 1973), and frequently comprise more than half of the fishes in trawls taken below a depth of 1000 meters.

Macrourids are most abundant on continental slopes between 500 and 2000 meters depth. The greatest number of species occur in the western Pacific (Gilbert and Hubbs, 1920). There are many extremes within the group with respect to distribution. Sampling of the deep ocean has not been complete in many areas of the world, so that some of the

anomalies of distribution may be artifacts of limited sampling rather than actual distribution. One species is known only from depths greater than 5000 meters in the eastern North Atlantic (Echnomacrurus mollis: Nybelin, 1957). Another was first described from a specimen that had washed up on a beach during a storm (Lepidorhynchus denticulatus: Richardson, 1846). Some have been caught over a great range of depths (Coryphaenoides armatus: 1600 to 4700 meters; Marshall and Iwamoto, 1973; Iwamoto and Stein, 1974), while others are limited in their depth range (Macrourus berglax: 200 to 600 meters; Marshall and Iwamoto, 1973).

The geographic range varies between species as well, with some of the deeper living species found in the Pacific, Atlantic, and Indian Oceans (Coryphaenoides armatus and Coryphaenoides leptolepis: Marshall and Iwamoto, 1973; Iwamoto and Stein, 1974). Sixteen species are known only from the Sulu Sea (Gilbert and Hubbs, 1920; Hubbs, 1930, 1954). One species has been caught only near Hawaii and in the North Atlantic (Nezumia bubonis: Iwamoto, 1974). Another is known only from Japan, the Gulf of Mexico, and the equatorial Atlantic (Squalogadus modificatus: Marshall and Iwamoto, 1973). These disjunct distributions may represent a lack of adequate sampling at the appropriate depths and bottom types, or a lack of suitable habitat in areas between the widely separated points where these two species have been found.

The abundance of macrourids and their dominance in the benthopelagic community has been demonstrated by the use of cameras set on the bottom to photograph animals attracted to bait (Isaacs, 1969; Isaacs and Schwartzlose, 1975; Dayton and Hessler, 1972). Large numbers of fish came to bait and showed great activity over several days in depths as great as 6000 meters. The distance travelled by the fish to bait is not known, so that density cannot be estimated from these photographs.

Photographic surveys and observations from submersibles have been used to study the distribution of macrourids over small areas (Barham, Ayer and Boyce, 1964; Marshall and Bourne, 1967; Grassle, Sanders, Hessler, Rowe and McLellan, 1975). The typical head-down pose of macrourids over the sediment surface was first described from photographs (Marshall and Bourne, 1964). The analysis of one series of photographs taken from a remote underwater manipulator revealed that the macrourid (Coryphaenoides acrolepis) common in the area appeared in photographs only in a few frames following the disturbance of sediment by the vehicle (Hessler, in preparation). It is apparently attracted to the sediment cloud or to the animals exposed when the sediment is disturbed.

## II. Trophic Ecology of the Macrouridae

It has been suggested that macrourids derive their nourishment from small animals inhabiting the sediments of the

deep ocean (Joubin, 1933; Marshall and Bourne, 1964). These suggestions were made on the basis of the specialized nature of macrourids and knowledge of the limits of their distribution at the bottom of the deep sea.

Recent studies of the stomach contents of several large macrourid species have shown that pelagic organisms are an important component of the diet of macrourids (Pearcy and Ambler, 1974; Haedrich and Henderson, 1974; Geistdorfer, 1973). Further comparison of the stomach contents of different species shows differences in the type of food ingested. In a study of the macrourids of Japan, Okamura (1970b) found that the proportion of benthic organisms in stomachs increased in an evolutionary sequence leading to the most specialized genus of the family, Coelorinchus. There are differences in the stomach contents of the five species of Coryphaenoides studied by Pearcy and Ambler (1974) with respect to benthic or pelagic origin of prey and size of prey.

The appearance of large numbers of macrourids and other animals at bait placed on the sea floor has led to the hypothesis that large pieces of detritus may serve as food for mobile scavengers that live near the sediment surface and can swim long distances to food (Dayton and Hessler, 1972; Isaacs and Schwartzlose, 1975). There has been little direct evidence from the stomach contents of macrourids, with the exception of one species, Coryphaenoides armatus, that large carcasses are an important food source. Remains of large

animals have been found in the stomachs of other fishes, notably sharks, caught near the bottom in fairly great depths (Clarke and Merritt, 1972).

There are some limitations in the study of stomach contents of macrourids to elucidate the role they play in benthic food chains. Macrourids have large swimbladders with no direct opening to the digestive tract or mouth. As fish are brought to the surface from depth, gas in the swimbladder expands and causes the stomach to evert through the mouth and thereby lose its contents. Stomach eversion occurs at different frequencies depending on the species and size of the specimens as well as on the depth and means of capture. It is difficult to tell the relation between prey organisms found inside stomachs and available prey without detailed information about all organisms of the same environment. This type of information is known in detail for only a few areas of the ocean (for example, Grassle et al., 1975). Generalizations about the influence of fish predation on their prey community must be made cautiously until there is detailed knowledge of the dynamics of the entire community.

### III. Systematics of the Macrouridae

The Macrouridae is allied with the Eretmophoridae, Gadidae, Melanonidae, Merlucciidae, Muraenolepidadae, and Steindachneriidae in the order Gadiformes, or Anacanthini (Marshall and Cohen, 1973). The Gadiformes has been included

with the Percopsiformes, Batrachoidiformes, Lophiiformes and Gobiesociformes in the superorder Paracanthopterygii (Greenwood, Rosen, Weitzman and Myers, 1966; Rosen and Patterson, 1969). The macrourids form a fairly distinct group within the Gadiformes. There are a few forms intermediate between the Merlucciidae and the Macrouridae (Marshall, 1966; Marshall and Cohen, 1973). The Macrouridae are a highly specialized group limited in distribution which have not given rise to any other groups of fishes.

The Macrouridae have been divided into four subfamilies, the Bathygadinae, Macruoroidinae, Tracyrincinae and Macrourinae (Marshall and Iwamoto, 1973). The first three of these subfamilies are quite distinct from each other and contain few species. The fourth subfamily includes most of the species of the family and can be divided into several groups of genera (Iwamoto, 1972). The evolutionary relationships between these generic groups are confusing because of the seeming convergence of two evolutionary lines (Okamura, 1970b).

The species level taxonomy of the macrourids has been thoroughly studied in the western North Atlantic (Marshall and Iwamoto, 1973), tropical Atlantic (Iwamoto, 1970), northern East Pacific (Iwamoto and Stein, 1974), central eastern Pacific (Iwamoto, in preparation) and Japanese waters (Okamura, 1970a) and Sulu Sea (Gilbert and Hubbs, 1916, 1920).

#### IV. Functional Anatomical Approach to Trophic Ecology

Many of the anatomical specializations of fishes are adaptations for the utilization of one type of food source or another. The comparative anatomy of the digestive system of teleosts has been studied with an interest in understanding feeding habits (Tyler, 1973; Geistdorfer, 1972). Gill raker structure, mouth size, and tooth morphology are often used to explain the type of food a fish is adapted to feed on.

The mechanical workings of the jaws of teleosts have been studied for the most part on relatively unspecialized fishes that can be easily kept alive in tanks of freshwater (Anker, 1974; Osse, 1969; Lauder, 1976). Analysis of highly specialized fishes can illustrate more clearly the functioning of anatomical features that are not so obvious in intermediate forms, and thus make the more generalized forms easier to understand (Liem, 1967).

Deep sea teleosts possess some of the most bizarre anatomical adaptations of any fishes. In addition, their feeding habits are often difficult to study because they cannot be kept in captivity and stomach content analysis is difficult when stomachs are frequently empty and few specimens have been caught. The feeding adaptations of some very specialized deep sea fishes have been examined through the study of the mechanics of their heads. Tchernavin (1953) described the functional anatomy of the viperfish, Chauliodus sloani, and was able to explain how C. sloani is capable

of capturing both very large and very small prey organisms. Differences in mouth size and gill raker structure of several melamphoids have been studied with regard to their importance in differences in predator strategy between species of different depths (Ebeling and Cailliet, 1974). The mechanics of the head of the chimaera, Callorhynchus capensis, and the contents of stomachs have been studied together to understand its evolutionary biology and ecology (Ribbink, 1971).

The Macrouridae are suited to a comparative study of jaw mechanics for several reasons. There are a great number of species within the family, nearly all of them live at the bottom of the deep sea, and there is a large variety in the morphology of the head, including several generalized forms and a number of specialized ones that show different specializations. There are only a few possibilities of available food in the environment of the macrourids, and they have been recorded to feed on most of the types of potential food. The extremes in the morphology of the head of the macrourids are likely to be specializations related directly to the ability to utilize the different food resources on the bottom of the ocean. The extreme specializations can also be used to explain the functional significance of characters of the more generalized species.

## METHODS

Preserved museum specimens were dissected, examined, photographed and drawn. For species where small specimens were available, trypsin-cleared and alizarin-stained preparations of the skeleton were made according to the method of Taylor (1967). Ligamentary-articulated dried skeletons were made from frozen and fresh specimens according to the method of Konnerth (1965).

The possible movements of the head were investigated by manipulating freshly caught specimens of Nezumia bairdii, Malacocephalus occidentalis, Coryphaenoides rupestris, Coryphaenoides armatus, Coryphaenoides leptolepis, Macrourus berglax and Coelorinchus coelorinchus carminatus during a cruise of the R.V. Gilliss during September 1975.

The contents of the stomachs of the study material were examined and identified.

## MATERIALS

The following list of specimens examined in this study is in the order in which they are considered here, which follows the phylogeny proposed by Okamura (1970b). \* denotes cleared and stained material and + denotes ligamentary articulated dried skeletons.

## MERLUCCIIDAE

Macruronus novaezelandiae

MCZ 48944, 4 specimens, 33-59 mm HL

MCZ 51164, 2 specimens, 37,41 mm HL

\*MCZ 51165, 1 specimen, 31 mm HL

## STEINDACHNERIIDAE

Steindachneria argentea

USNM 188852, 3 specimens, 37-43 mm HL

## MACROURIDAE

## Bathygadinae

Bathygadus macrops

UMML 15193, 3 specimens, 68-69 mm HL

+MCZ 51168, 1 specimen, 79 mm HL

## Macrourinae

Lepidorhynchus denticulatus

MCZ 51515, 4 specimens, 53-63 mm HL

Malacocephalus occidentalis

UMML 25600, 3 specimens, 47-51 mm HL

\*MCZ 51471, 3 specimens, 21-26 mm HL

+MCZ 51167, 1 specimen, 68 mm HL

Nezumia bairdii

MCZ 51167, 7 specimens, 46-65 mm HL

\*MCZ 51174, 2 specimens, 21, 32 mm HL

+MCZ 51466, 1 specimen, 61 mm HL

Mataeocephalus acipenserinus

USNM 55249, 3 specimens, 40-43 mm HL

USNM 126542, 2 specimens, 42, 50 mm HL

Coryphaenoides rupestris

VIMS 00899, 3 specimens, 40-43 mm HL

MCZ 51172, 3 specimens, 114-133 mm HL

+MCZ 51462, 1 specimen, 142 mm HL

Coryphaenoides carapinus

MCZ 51178, 15 specimens, 23-52 mm HL

MCZ 51864, 1 specimen, 54 mm HL

\*MCZ 51177, 1 specimen, 37 mm HL

Coryphaenoides armatus

MCZ 51868, 1 specimen, 78 mm HL

\*MCZ 51470, 1 specimen, 31 mm HL

+MCZ 51154, 1 specimen, 118 mm HL

+MCZ 51464, 1 specimen, 99 mm HL

Coryphaenoides acrolepis

MCZ 51931, 1 specimen, 156 mm HL

MCZ 51932, 3 specimens, 57-77 mm HL

\*MCZ 51933, 1 specimen, 35 mm HL

Coryphaenoides leptolepis

MCZ 51155, 2 specimens, 66,78 mm HL

+MCZ 51465, 1 specimen, 98 mm HL

Coryphaenoides pectoralis

MCZ 51930, 2 specimens, 98,110 mm HL

Macrourus berglax

MCZ 37779, 1 specimen, 90 mm HL

VIMS 03536, 1 specimen, 130 mm HL

+MCZ 51463, 1 specimen, 145 mm HL

Abyssicola macrochir

USNM 77248, 3 specimens, 68-75 mm HL

Coelorinchus coelorinchus carminatus

UMML 13169, 1 specimen, 66 mm HL

+MCZ 51169, 1 specimen, 59 mm HL

Coelorinchus chilensis

LACM Eltanin 1989, 3 specimens, 42-51 mm HL

Coelorinchus longissimus

MCZ 47740, 1 specimen, 57 mm HL

Coelorinchus occa

UMML 26794, 1 specimen, 133 mm HL

+MCZ 51166, 1 specimen, 117 mm HL

Coelorinchus jordani

USNM 77197, 2 specimens, 49,51 mm HL

Coelorinchus innotabilis

LACM Eltanin 1718, 3 specimens, 52-55 mm HL

Coelorinchus japonicus

SU 7939, 2 specimens, 97,121 mm HL

## Trachyrincinae

Trachyrincus helolepis

SOSC Reg. No. 309, 3 specimens, 96-98 mm HL

## ABBREVIATIONS

mm millimeter

HL head length

## Institutional Abbreviations

LACM Los Angeles County Museum

MCZ Museum of Comparative Zoology

SOSC Smithsonian Oceanographic Sorting Center

SU Stanford University collections, housed at the California  
Academy of Sciences

UMML University of Miami, Rosenstiel School of Marine and  
Atmospheric Sciences

USNM United States National Museum

## ANATOMICAL ABBREVIATIONS

AAP	Adductor arcus palatini
AM1 $\alpha$	Adductor mandibulae 1 $\alpha$
AM1 $\beta$	Adductor mandibulae 1 $\beta$
AM1 $\beta'$	Adductor mandibulae 1 $\beta'$
AM $\omega$	Adductor mandibulae $\omega$
AM2	Adductor mandibulae 2
ALV	Alveolar process of the premaxilla
ART	Articular process of the premaxilla
ASC	Ascending process of the premaxilla
CL	Cleithrum
DO	Dilatator operculi
ECT	Ectopterygoid
ENT	Entopterygoid
EPO	Epiotic
EPX	Epaxial muscles
FR	Frontal
GH	Geniohyoideus muscle
HPX	Hypaxial muscle
HAB	Hyohyoidei abductores muscle
HAD	Hyohyoidei adductores muscle
HMX	Head of the maxilla
HY	Hyoid
HYM	Hyomandibular
IB	Infraorbital bones

IFS    Infraorbital shelf

IM     Intermandibularis muscle

IML    Interopercular-mandibular ligament

IOP    Interopercle

LAC    Lacrimal

LAP    Levator arcus palatini

LO     Levator operculi

LP     Lip

MN     Mandible

MPL    Ligament between the maxilla and postmaxillary process  
       of the premaxilla

MTP    Metapterygoid

MX     Maxilla

NA     Nasal

OP     Opercle

PF     Prefrontal

PMX    Premaxilla

PMX CON   Premaxillary condyle of the maxilla

PR     Parietal

PRL    Primordial ligament

PRL PROC   Primordial ligament process of the maxilla

PSTMX   Postmaxillary process of the premaxilla

PTO    Pterotic

Q     Quadrangle

RC     Rostral cartilage

RMX    Ramus of the maxilla

SH Sternohyoideus  
SOC Supraoccipital  
SOP Subopercle  
SPO Sphenotic  
SYM Symplectic  
UHY Urohyal

Scale bars indicate 1 centimeter unless otherwise noted.

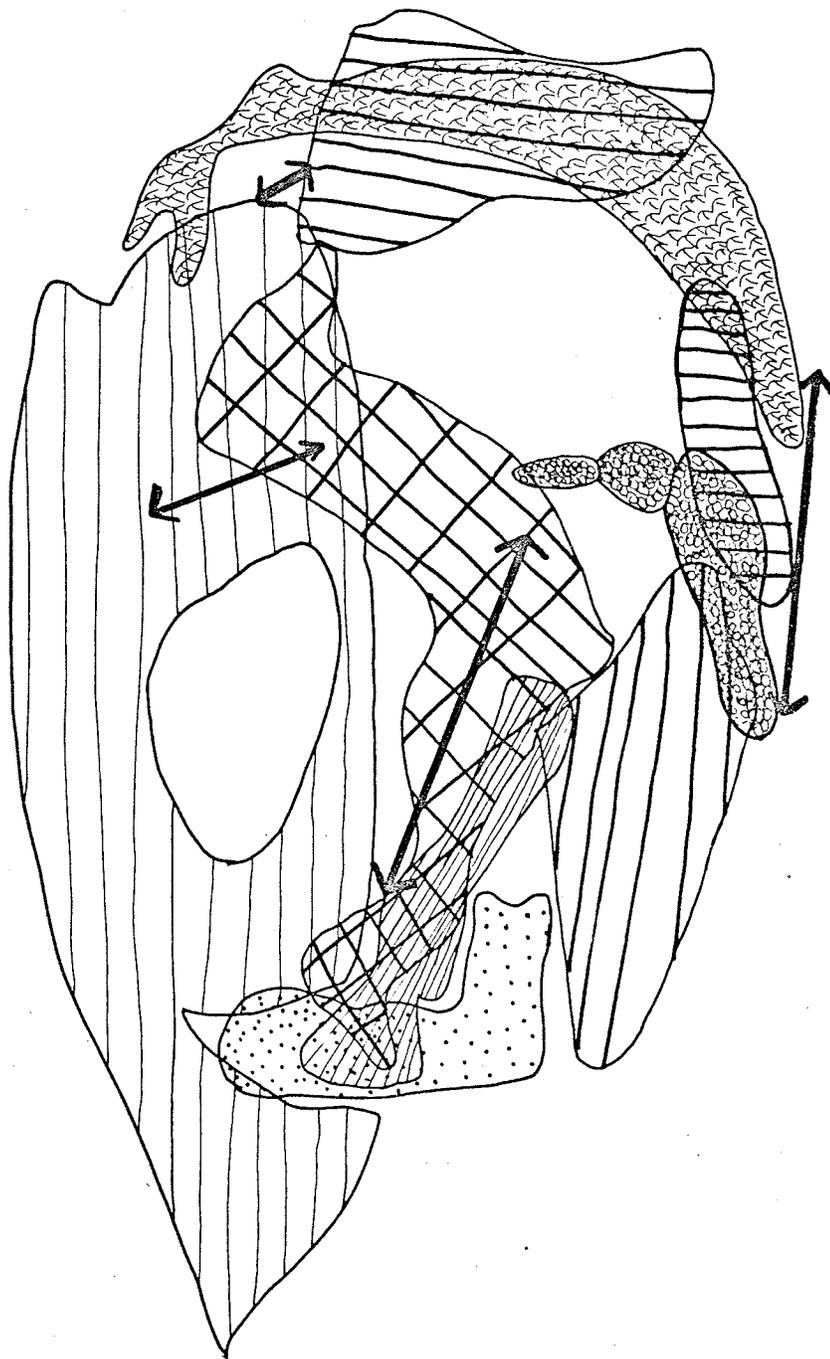
## GENERAL MODEL OF THE MACROURID HEAD

The highly kinetic head of teleosts consists of several mechanical units and couplings which interact to perform the functions of gill ventilation and feeding (Liem, 1967, 1970; Tchernavin, 1953). The functional dependence of structural complexes must be considered when explaining the adaptations to feeding on different food resources and the constraints of the extremes of adaptation. A description of the mechanical units and their possible movements will be followed by the description of the couplings responsible for the motions of feeding. The illustrations for the general model are based primarily on Macrourus berglax, a large species intermediate in many ways between the two large genera Coryphaenoides and Coelorinchus, to be considered in greater detail in the following chapter.

The mechanical units of the head of macrourids are: 1) cranium, 2) suspensorium, 3) opercular series, 4) jaws, 5) hyoid, and 6) pectoral girdle (figure 1). The gill arches are also an important component in the mechanics of the head in feeding and respiration.

The cranium of macrourids is low and broad, and is characterized in many species by a long rostrum anterior to the mouth formed by the paired nasal bones. Several

Figure 1. Diagram of the mechanical units of the head of a macrourid with the mouth closed. Arrows indicate couplings important in opening the mouth. Cranium-narrow horizontal lines; suspensorium-heavy crossed lines; premaxilla-dots; maxilla-diagonal lines; mandible-heavy horizontal lines; opercular series-vertical lines; hyoid-circles; pectoral girdle-narrow crossed lines.



bones form a rigid case that surrounds the brain; these include the alisphenoid, sphenotic, pterotic, epiotic, parietal, prootic, opisthotic, exoccipital, basioccipital, and supraoccipital (Okamura, 1970b, p.54). The supraoccipital forms a median keel at the posterodorsal side of the braincase, the supraoccipital crest, which is the site of insertion of some of the epaxial muscles (figure 2: SOC). Contraction of these muscles raises the cranium and the first few vertebrae (Tchernavin, 1953).

Anterior to the braincase the orbits are bordered dorsally by the wide frontals and medially by the parasphenoid. Anterior to the frontals are the nasals, and anterior to the parasphenoid and ventral to the nasals are the vomer and ethmoid. The prefrontal extends from the point where the frontals and nasals meet ventrally to border the anterior margin of the orbit.

The suspensorium is roughly triangular in shape and is suspended from the cranium at two points, the palatine and hyomandibula. The other bones of the suspensorium are the endopterygoid, ectopterygoid, metapterygoid, quadrate, sympectic, and preopercle (figure 3). The suspensorium forms the roof of the mouth and the floor of the orbit as well as part of the lateral surface of the head posterior to the orbit. The levator arcus palatini muscle (figure 5) extends from the postorbital region of the cranium to the anterodorsal edge of the preopercle and

Figure 2. Lateral view of the skull of Macrourus  
berglax, MCZ 51463, 145 mm HL.

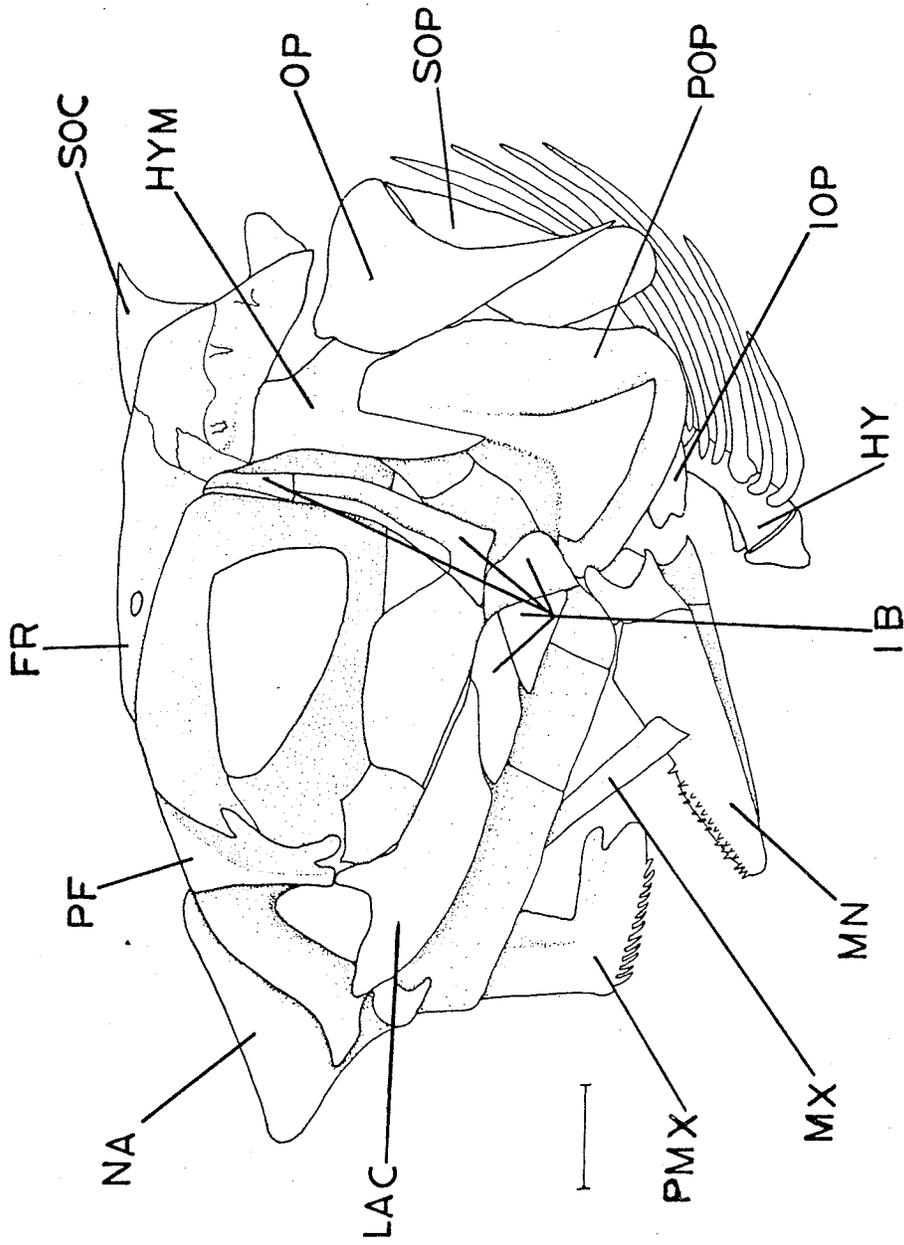


Figure 3. Lateral view of the suspensorium of  
Macrourus berglax, MCZ 37779, 90 mm HL.

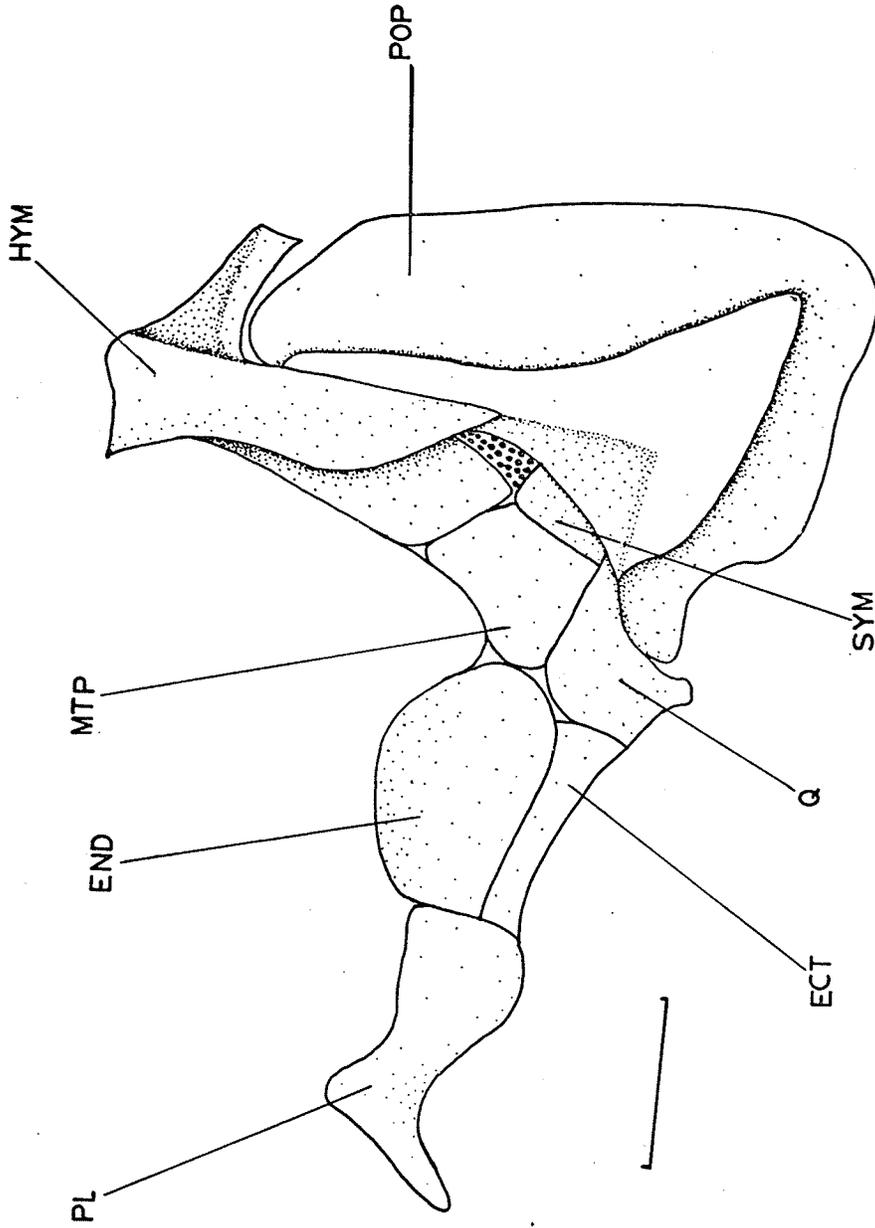
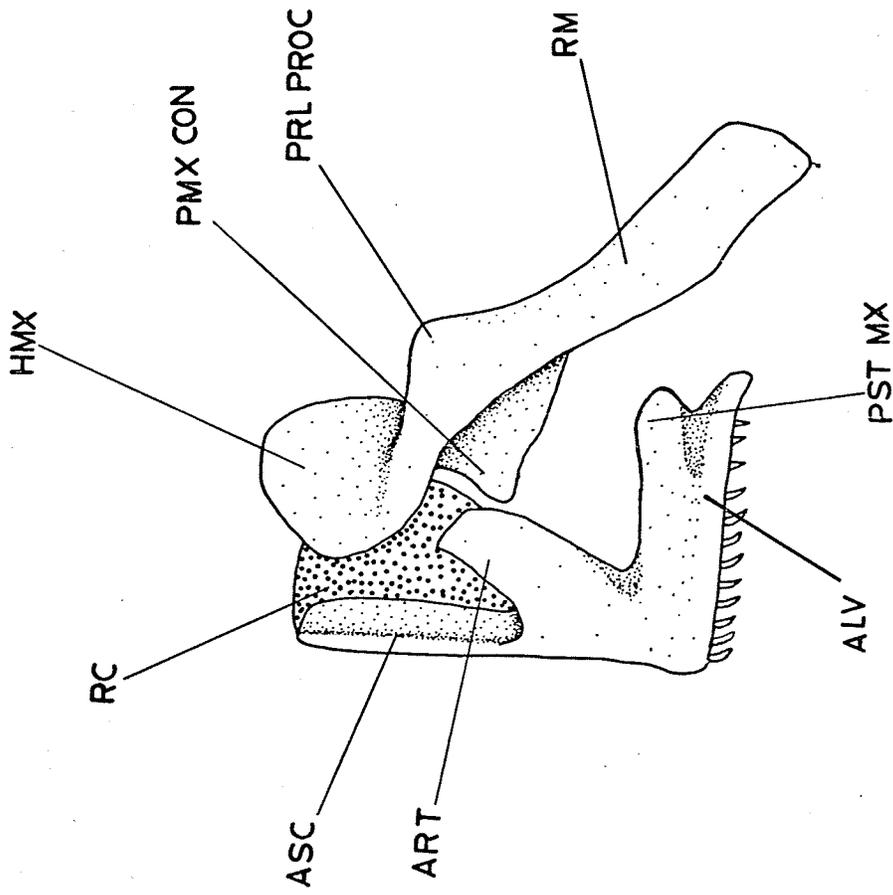


Figure 4. Lateral view of the premaxilla and maxilla of Macrourus berglax, MCZ 37779, 90 mm HL.



its contraction makes the ventral corner of the suspensorium move laterally. The opposite motion results from the contraction of the adductor arcus palatini muscle, which extends from the parasphenoid to the endopterygoid. The preopercle is firmly held to the hyomandibula, symplectic, and quadrate and is functionally a part of the suspensorium rather than the opercular series. Part of the anterior edge of the preopercle appears folded back over the posterior portion of the bone forming the preopercular shelf. In some species, the preopercular shelf forms part of a pronounced infraorbital ridge. The opercular series, posterior to the suspensorium, consists of three elements, the opercle, subopercle, and interopercle (figure 2: OP, SOP, IOP). The small, triangular opercle is dorsal and lateral. It articulates anteriorly with the hyomandibula and there are two muscles from the cranium to its medial surface. The dilatator operculi inserts anterior to the hyomandibular articulation and the levator operculi posterior to it. The subopercle is a flat oval attached to the ventromedial surface of the opercle by syndesmosis. The interopercle, ventral and anterior to the subopercle, is a thin oval in some species and a smaller thicker rectangle in others (Okamura, 1970b, p.45-53). The interopercle has a strong ligamentous connection from its anterior edge to the posteroventral corner of the mandible and from its medial surface to the epihyal. The subopercle and interopercle

are connected by some very loose connective tissue.

The upper jaw consists of the premaxilla and maxilla (figure 4). In lateral view the premaxilla is L-shaped, with a vertical ramus consisting of the anterior ascending process and the shorter articular process. The horizontal arm composed of the long alveolar process bearing a small postmaxillary process dorsally. The large rostral cartilage is held between the ascending and articular processes; it slides dorsoventrally against the vomer as the mouth opens. When the mouth is closed the ascending processes and rostral cartilage fit into a cavity in the cranium formed dorsally by the nasala and laterally and anteriorly by the lacrimals. There is a strong ligament from the distal end of the ascending process of the premaxilla to the base of the maxillary process of the palatine. In some species the loose connective tissue between the alveolar process of the premaxilla and the maxilla is differentiated into a ligament from the postmaxillary process to the distal end of the maxilla.

The maxilla, posterior and dorsal to the premaxilla, has a broad head anteriorly that articulates with the palatine, vomer, and premaxilla. The slender maxillary process of the palatine fits into a broad groove on the lateral surface of the maxilla. Ventral to the articulation with the palatine is a medial process, the premaxillary condyle, that articulates with the articular process of the

premaxilla through a meniscus of cartilage. The anteromedial surface of the maxilla articulates with the vomer. The ethmo-maxillary ligament extends from the lateral surface of the head of the maxilla dorsally to the anterior surface of the ethmoid. The short broad maxilomandibular ligament runs from the medial surface of the distal end of the maxilla to the lateral surface of the ascending process of the mandible. The lip is an external ligament that connects the distal ends of the maxilla and premaxilla with the mandible anteriorly. The primordial ligament runs from the maxilla just posterior to the palatine articulation to the lateral surface of the mandible ventral to the ascending process. Two subsections of the adductor mandibulae complex originate posteriorly on the suspensorium and insert on the maxilla. Adductor mandibulae 1  $\alpha$  inserts on the primordial ligament, and adductor mandibulae 1  $\beta$  inserts on the medial surface of the premaxillary condyle (figure 5).

The mandible consists of the dentary, articular, and angular, held together by syndesmoses, in the shape of a shallow triangle. The dorsal apex of the triangle is the ascending process, and along the posterodorsal edge of this process is the articulation with the quadrate. Adductor mandibulae 2 originates on the hyomandibula and metapterygoid and runs ventrally to its insertion, through connective tissue, on adductor mandibulae  $\omega$  medial to the ascending process of the mandible (figure 6). Adductor

Figure 5. Lateral view of the superficial cheek  
muscles of Macrourus berglax, MCZ 37779, 90 mm HL.

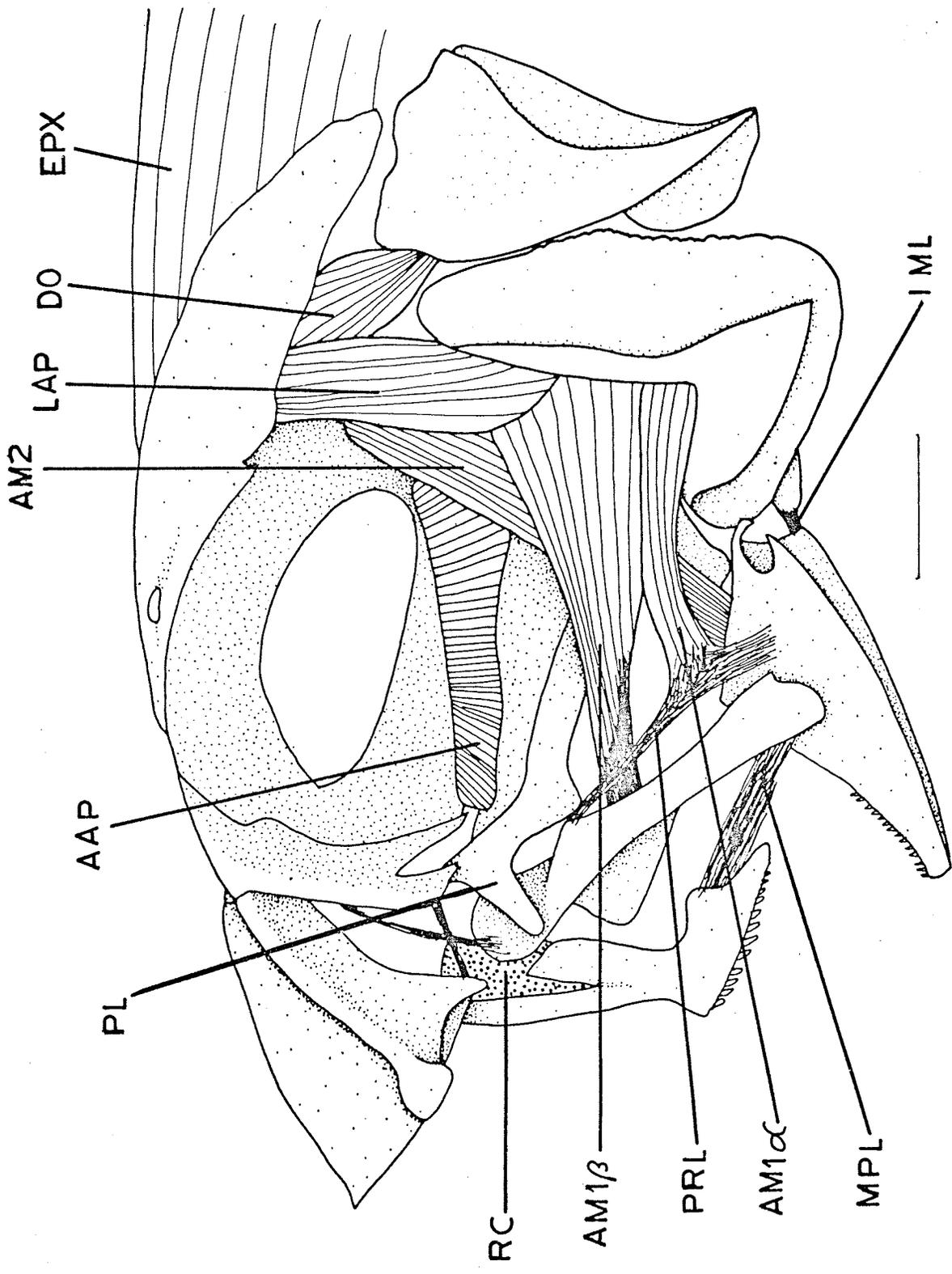
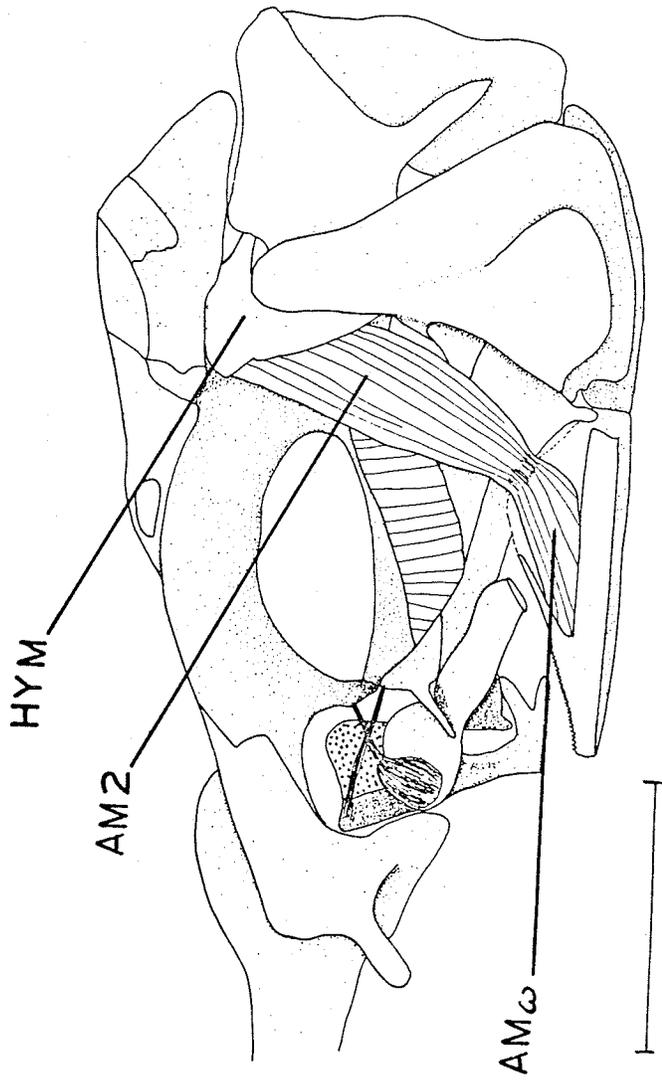


Figure 6. Lateral view of the deep cheek muscles of Mataeocephalus acipenserinus, USNM 126542, 50 mm HL.

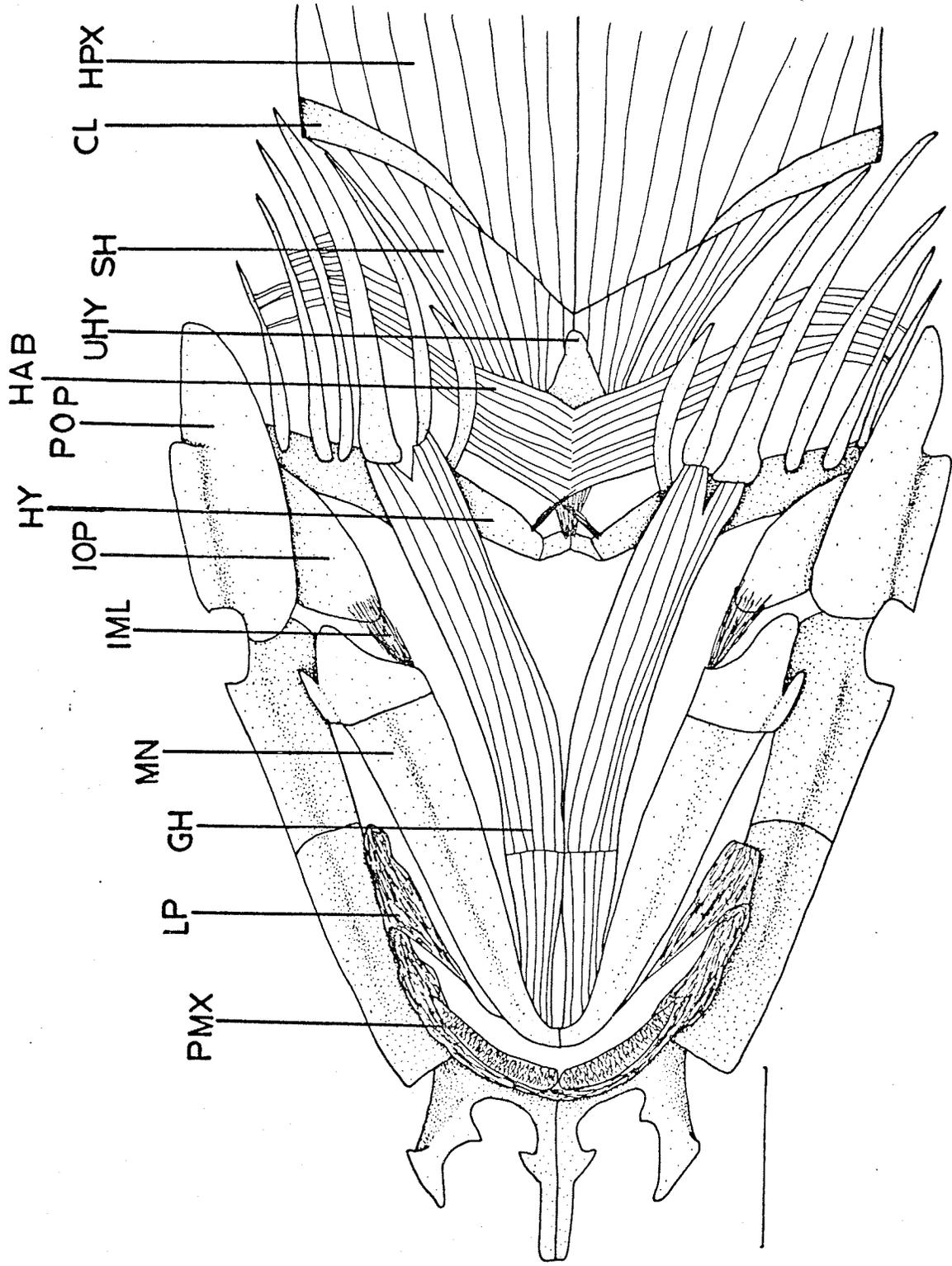


mandibulae  $\omega$  inserts in a pocket of the medial surface of the dentaries anteriorly. The mandible can rotate ventrally around the quadrate. The two halves of the mandible can spread laterally a small distance from each other through the widening of the angle where the dentaries meet.

The hyoid apparatus consists of two bars held together at their antero-ventral symphysis, extending dorsoposteriorly via the ceratohyal and epihyal to the interhyal, which articulates with the suspensorium. In ventral view the hyoid forms a V (figure 7), and the anterior point can move posteriorly so that the two bars spread to expand the oral cavity laterally. The geniohyoideus muscle runs on each side from the mandible near the dentary symphysis to the s ceratohyal and two branchiostegal rays. The anterior and posterior sections of this muscle are innervated by different nerves and the two parts can contract independently of one another (Osse, 1969). The anterior section is active during the closing of the mouth and the posterior section can contract during opening. The functional name protractor hyoidei has been used for this muscle (Winterbottom, 1974), but is not appropriate in view of the evidence that it has functions other than the protraction of the hyoid (Osse, 1969).

The pectoral girdle extends from the posteroventral corner of the cranium ventrally around the sides of the body posterior to the gill openings, to a point along the ventral midline where the two sides meet. The bones of the pectoral

Figure 7. Ventral view of the head of Coelorinchus  
coelorinchus carminatus, UMML 13169, 66 mm HL.



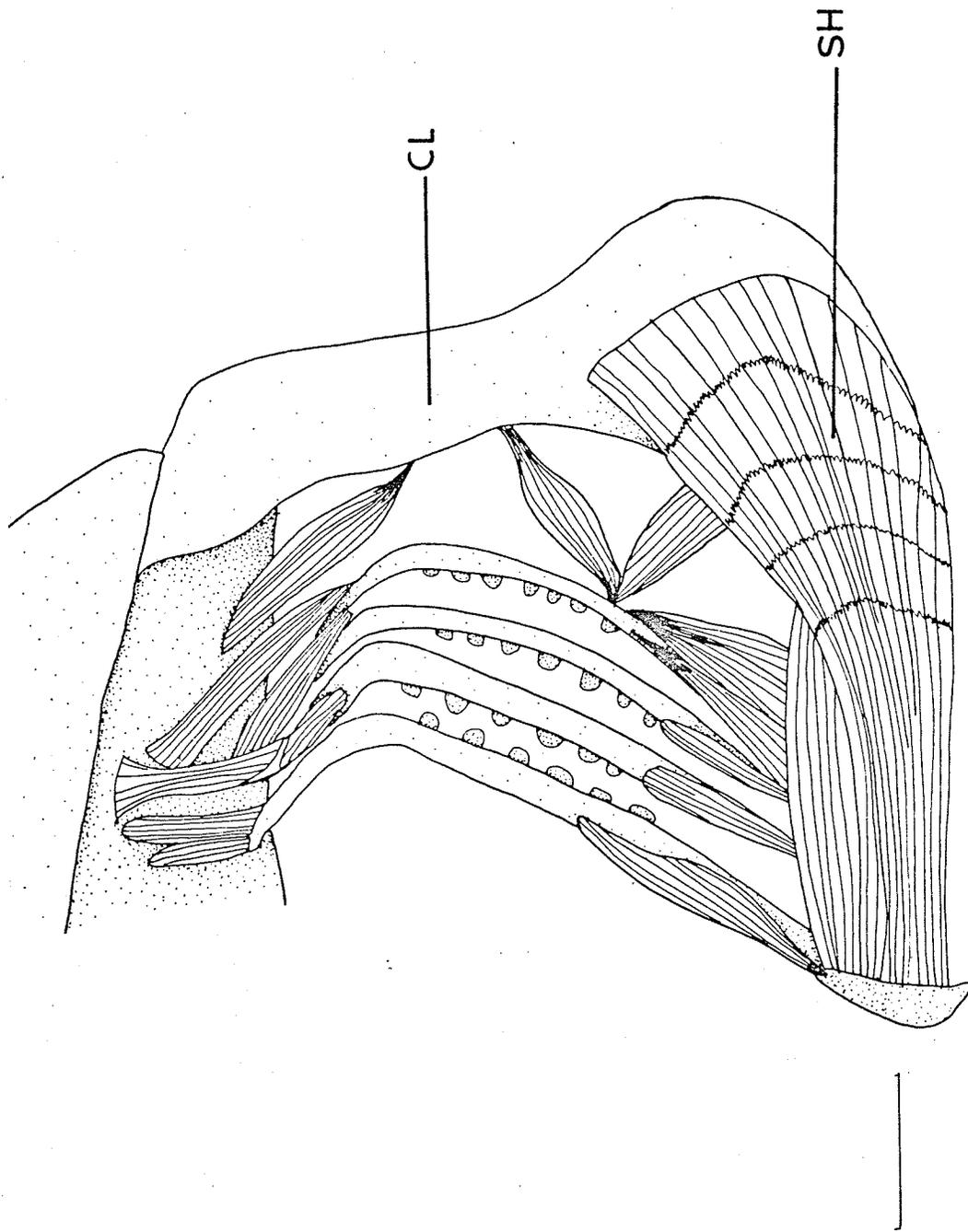
girdle are: posttemporal, supracleithrum, cleithrum, postcleithrum, scapula and coracoid (Okamura, 1971; p. 89). The pectoral girdle is capable of swinging anteroposteriorly from the cranium. The wide and deep sternohyoideus muscle originates on the anterior surface of the cleithrum and extends to the hyoid symphysis. The hypaxial muscles insert on the posterior surface of the cleithrum and extend anteriorly in a thin layer ventral to the sternohyoideus.

The gill arches are the supporting elements for the gill filaments, where exchange of carbon dioxide and oxygen occurs, and form a posterior set of "jaws" around the alimentary canal between the mouth and esophagus. There are tooth plates dorsally and ventrally that can grasp food and push it into the esophagus. The gill arches are suspended by muscles from the cranium, pectoral girdle and hyoid. The muscles of the gill arches of macrourids are illustrated in figure 8.

#### I. Movements of the Head During Feeding

Several motions of the elements of the macrourid head occur as the mouth is opened for feeding. The mandible is depressed, the premaxilla protruded, the head is lifted, and the volume of the oral cavity is increased by the depression of hyoid and the abduction of the suspensoria. The sequence of these movements cannot be determined from preserved specimens, and a small motion of one element can greatly influence the result of another movement, so that combinations of possibilities of movements during feeding are too

Figure 8. Lateral view of the pharyngeal muscles of Coelorinchus occa, UMML 26794, 133 mm HL.



great to enumerate. The major couplings responsible for opening the mouth to its fullest are discussed here and this is admittedly a simplification of the actual processes.

One major coupling responsible for the lowering of the mandible is the sternohyoideus-hyoid-interopercle-mandible coupling. Contraction of the sternohyoideus pulls the hyoid symphysis caudally, causing the two hyoid bars to spread laterally and rotate so that the symphysis moves ventrally. The interopercle is firmly attached to the epihyal and is pulled posteroventrally with the hyoid. This results in a pull on the posteroventral corner of the mandible where the interoperculo-mandibular ligament inserts, so that the mandible rotates around the quadrate and anterior end of the mandible moves ventrally. The result of pulling on the sternohyoideus muscle in a freshly caught specimen is shown in figure 9. The mandible is depressed somewhat and the cavity is expanded ventrally, but the mouth is not fully open.

The coupling of the epaxial muscles-cranium-suspensorium involves the lifting of the head by the contraction of the epaxial muscles. This results in a number of things: the suspensorium is lifted with the cranium, so that the anterior corner (palatine) is lifted and brings with it the maxilla and premaxilla, and the quadrate rotates anteriorly a small distance so that the mandible is depressed. Figure 10 shows the result of pulling on the epaxial muscles in a fresh specimen. Lifting the cranium away from the mandible results

Figure 9. Freshly caught specimen of Macrourus berglax, VIMS 03536, sternohyoideus muscle pulled in the direction indicated by arrow.



Figure 10. Freshly caught specimen of Macrourus berglax, VIMS 03536. Epaxial muscles just posterior to the head are pulled in the direction indicated by arrow.



in about the same amount of mandibular depression as pulling on the sternohyoideus.

A third coupling, the levator operculi-opercular series mandible coupling has been shown to be important in mandibular depression in other teleosts (Liem, 1970; Osse, 1969). The contraction of the levator operculi pulls the opercle dorsally, and through a series of ligaments, pulls the subopercle, interopercle and interopercular-mandibular ligament so that the mandible rotates around the quadrate and opens. In macrourids the levator operculi is small and there is only a weak ligamentous connection between the subopercle and interopercle, so that this coupling is probably not very important in the opening of the mouth.

As the mandible is lowered, the premaxilla protrudes and the maxilla swings anteroventrally. It is possible that this motion is a result of pulling through the maxillo-mandibular ligament (Schaeffer and Rosen, 1961; Liem, 1970). Pulling on the sternohyoideus and on the epaxial muscles resulted in the lowering of the mandible, but the premaxilla did not move to the full limit of its protrusibility (figures 9 and 10). Ballintijn, van den Burg and Egberink (1972) have shown that the contraction of one of the adductor mandibulae muscles attached to the maxilla influenced the angle at which the premaxilla was protruded in the carp. Pulling on the primordial ligament at the insertion of adductor mandibulae 1 resulted in the protrusion of the premaxilla in a fresh

specimen (figure 11). The primordial ligament inserts on the maxilla on a high process posterior to the palatine articulation, and pull on this point from a ventoposterior angle caused the maxilla to rotate around the palatine so that the head of the maxilla moved ventrally and its rotation pushed the rostral cartilage and the premaxilla ventrally. Other factors may also influence the protrusion of the premaxilla, such as the ligaments from the premaxilla and rostral cartilage to the palatine and maxilla, respectively, and the interactions which occur when the cranium is lifted.

The major coupling responsible for the lateral expansion of the mouth is the levator arcus palatini-suspensorium, which directly causes the suspensorium to swing laterally. This results in the lateral movement of the quadrate, which causes the dentaries to move apart from each other a little, and the mandible to drop. Another result of suspensorial abduction is the change in angle of the hyoid so that the sternohyoideus is more effective in pulling the hyoid caudally (Osse, 1969). The other means of expanding the volume of the mouth is the depression of the hyoid, already mentioned in the sternohyoid-hyoid-interpercle coupling.

The couplings for closing the mouth (figure 12) reverse the motions of opening, though not in the same sequence, as this would result in the expulsion of the water and food drawn into the mouth (Nyberg, 1971). The contraction of adductor mandibulae 2 and adductor mandibulae  $\omega$  results in

Figure 11. Macrourus berglax, VIMS 03536, freshly caught specimen. Primordial ligament pulled in direction indicated by arrow.

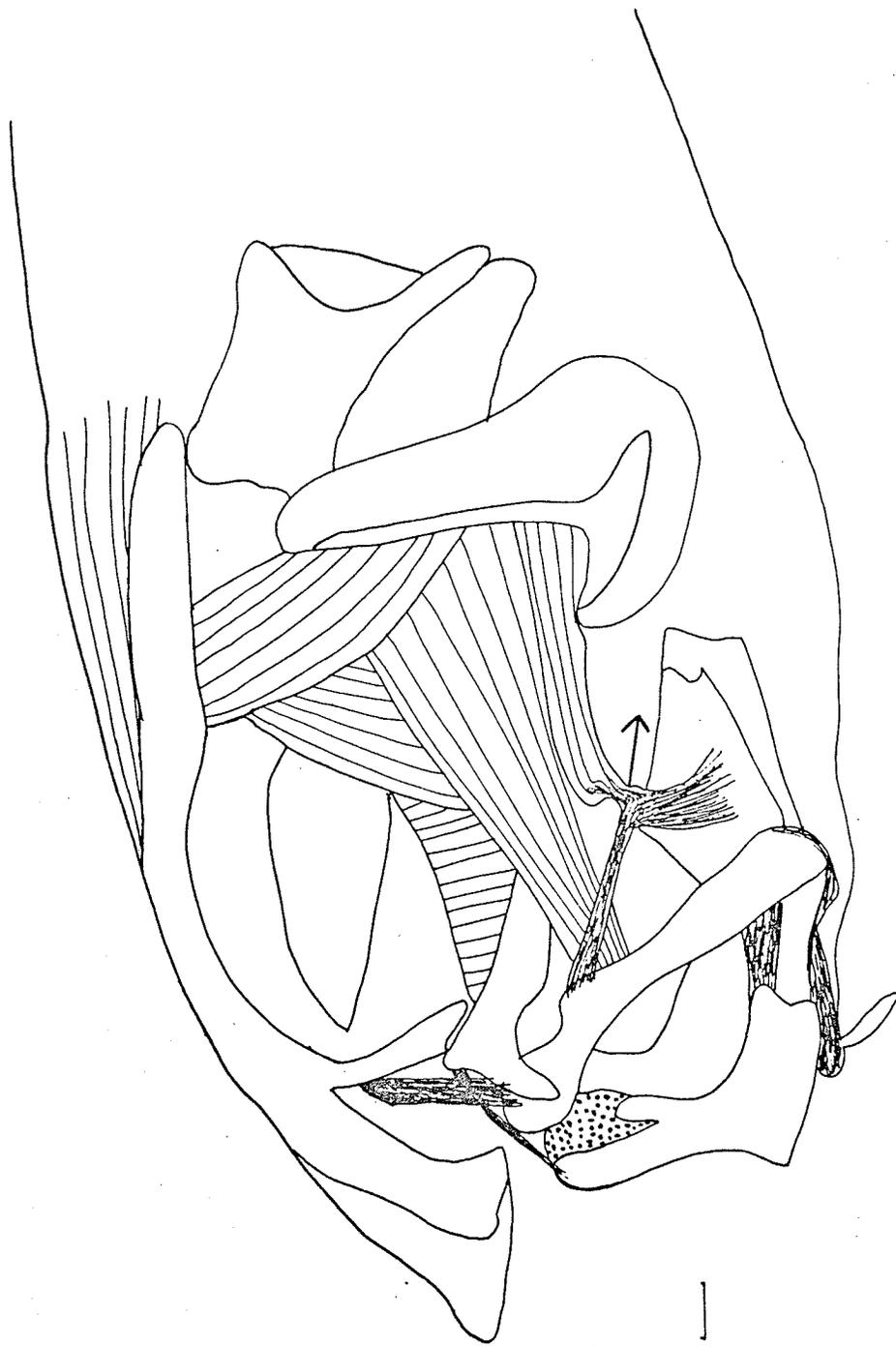
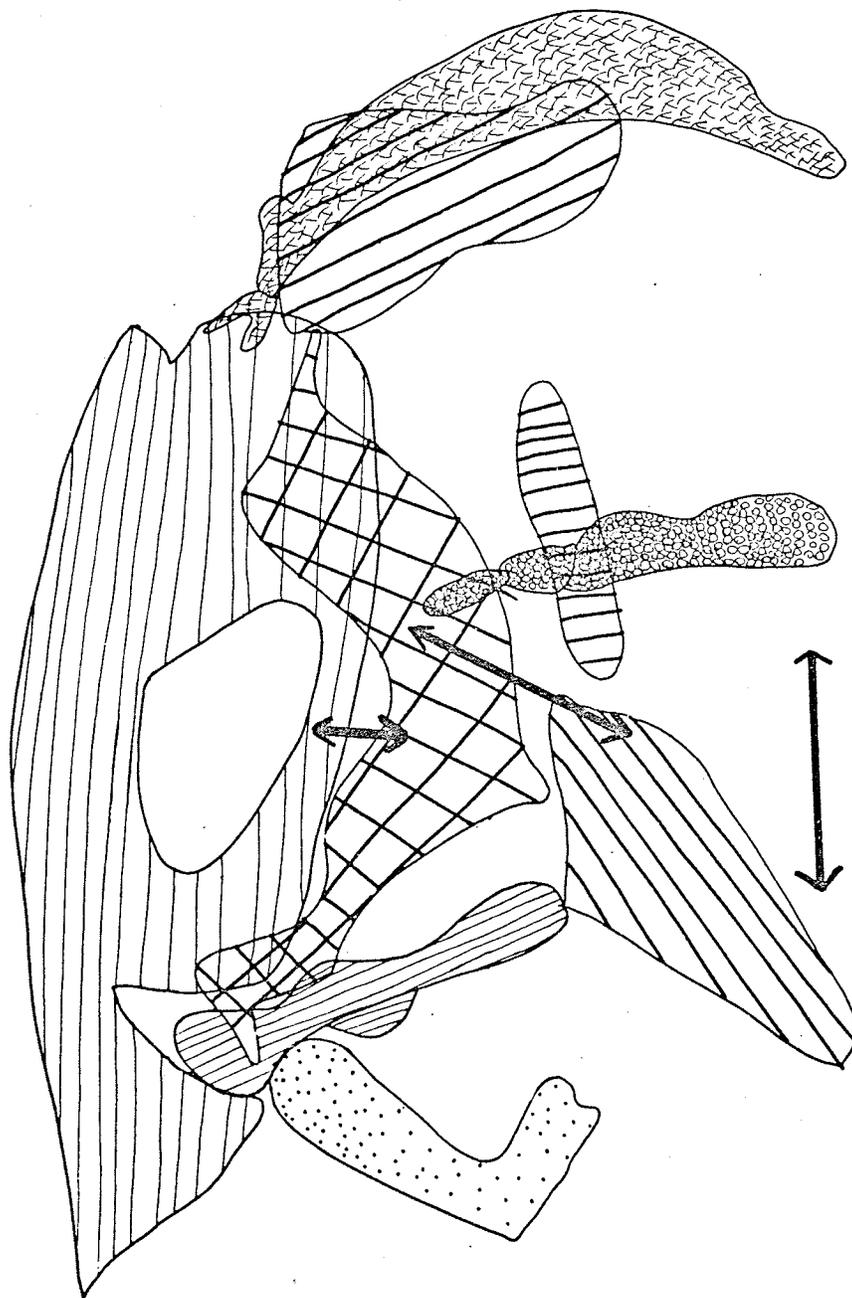


Figure 12. Diagram of the mechanical units of the head of a macrourid with the mouth open. Arrows indicate couplings for closing the mouth. Cranium-narrow horizontal lines; suspensorium-heavy crossed lines; premaxilla-dots; maxilla-diagonal lines; mandible-heavy horizontal lines; opercular series-vertical lines; hyoid-circles; pectoral girdle-narrow crossed lines.



bringing the distal end of the mandible dorsally and posteriorly. The geniohyoideus contracts and draws the dentaries and hyoid together. As long as the quadrato-mandibular articulation lies dorsal to the geniohyoideus, this results in the closing of the mandible.

The suspensorium returns to its closed position by the contraction of the adductor arcus palatine muscle. The lifted cranium is returned to its position of rest by the action of some of the body musculature.

The actual movements of the head of macrouids are far more complex than the simple model presented here. There are many possibilities for the contraction of several muscles at one time or in sequence, so that there is flexibility in the positions possible that are short of fully expanded. There is also a great deal of variation between the species of the family in the amount of protrusibility of the upper jaw, the extent of lateral expansion of the head, the architecture of the rostrum and probably in the means of creating suction.

## ANATOMY OF THE MACROURIDAE

The species examined represent some of the variety within the Macrouridae, chosen for their distinctiveness within the family, ecological importance and availability both in systematic collections and as freshly caught material. Two species formerly placed in the Macrouridae are included because of their presumed primitive status and intermediacy between the Macrouridae and Merlucciidae.

All of the fishes examined share a number of characteristics which have been used to unite them in a fairly well-defined taxonomic category. Many aspects of the overall body shape and head structure are also shared with fishes of other systematic affinities living in the same environment. All macrourids have large heads with large lateral line canals, short bodies and long, tapering tails. (The tail of macrourids is defined as that part of the body posterior to the anus (Iwamoto, 1970).) There are two dorsal fins, the first short and high and the second long and low, meeting the anal fin at the distal end of the tail. There is no true caudal skeleton, except in Trachyrincus (Marshall and Iwamoto, 1973). The pectoral fins are small and high on the sides of the body. The pelvic fins are small and thoracic. Most species have a mental barbel.

## I. Species Examined

Macruronus novaezelandiae is one of five species of Macruronus, originally placed in the Macrouridae and now placed in the Merlucciidae because of a number of anatomical characters in which it is more similar to Merluccius than to any macrourid (Marshall, 1966; Marshall and Cohen, 1973).

The head is not particularly large, nor is the tail as long and thin as in macrourids. It is known from shallow marine waters near New Zealand, and was first described from a specimen found washed up on a beach (Hector, 1870). The eyes are large, the scales are small and most of the head is without scales.

Steindachneria argentea is a monotypic genus known only from the Gulf of Mexico (Parr, 1946). Marshall (1966) removed it from the Macrouridae to place it in the Merlucciidae, and Marshall and Cohen (1973) created the family Steindachneriidae for this one species alone. The body is laterally compressed and is shorter and stouter than that of Macruronus. There is luminescent tissue covering the ventral part of the body and head (Cohen, 1964). The scales are small, the eyes are moderate and the mouth is large and terminal with large teeth.

Bathygadus macrops is one of more than twenty species of the two genera of the subfamily Bathygadinae. It has been caught in the tropical Atlantic at depths between 300 and 700 meters (Iwamoto, 1970). It resembles the merlucciids in having a blunt snout and large, terminal mouth, but differs from them in having wide bands of minute teeth and a number of other

characters. The eyes of B. macrops are fairly large, while those of the other species of the subfamily are small. There is no luminescent tissue known.

Lepidorhynchus denticulatus is a moderate sized species known only from waters south of New Zealand and Australia (Marshall and Iwamoto, 1973). It has been placed in the subfamily Macrourinae together with the majority of species of the family. By virtue of having six branchiostegal rays (rather than seven) it has been allied with Coryphaenoides and Coelorrinchus (Marshall and Iwamoto, 1973), but it is distinct in many ways from all other macrourids. It shares with Steindachneria having striated, luminescent tissue over the ventral third of the body and head. The establishment of its relationships within the family await further investigation. The mouth is large and terminal with large, widely spaced teeth. The eyes are large and the snout is small and blunt. The scales on the body are moderately large and have no pronounced keels; the condition of scales on the head could not be determined because of the battered condition of the specimens available. It has been caught in shallow waters to a depth of 100 meters (Hector, 1872) and the first specimen described was found thrown up on a beach (Richardson, 1846).

Malacocephalus occidentalis is a species of moderate size known from the north Atlantic (Marshall and Iwamoto, 1973). The generic status of this species within the natural species group tribe Malacocephalini (Iwamoto, 1972)

is uncertain and it is sometimes referred to as Ventrifossa occidentalis (Marshall and Iwamoto, 1973). The body is deep and somewhat compressed, and there is a small rostrum projecting anteriorly beyond the moderately large mouth. There are moderately large eyes, a long barbel and a small ventral light organ around the peritroct and anterior to it. The teeth of the upper jaw are large and separated in the outer row. Scales over the head and body are small.

Nezumia bairdii is common in the western North Atlantic at depths of 200 to 700 meters (Marshall and Iwamoto, 1973). It is a small species with large eyes and a moderate barbel. There is a small ventral light organ similar to that of Malacocephalus occidentalis. The rostrum is strong and high with large, specialized scales on the three corners. The mouth is small and inferior, with small teeth in wide bands. Scales are moderately large and bear small spines; those on the pronounced ridges of the head are no larger than over the rest of the head and body.

Mataeocephalus acipenserinus is a small species from Hawaii. It has a long rostrum and large scales along the ridges of the head and the three anterior corners of the rostrum. The mouth is very small and inferior. Eyes are moderate, a small ventral light organ is present, and there is a small barbel. Mataeocephalus tenuicauda, from the eastern Pacific, was also examined.

The genus Coryphaenoides in the sense of Okamura (1970a)

and Iwamoto and Stein (1974) is the largest in the family with some 65 species. Studies of the macrourids of the Atlantic have recognized several genera in addition to Coryphaenoides (Parr, 1946; Marshall and Iwamoto, 1973). This may be due to the fact that the representatives of the species group in the Atlantic fall into several distinct groups, while there are several species intermediate to the Atlantic genera in the Pacific. Coryphaenoides rupestris, the type species for the genus, is quite distinct from all others placed in Coryphaenoides, and perhaps ought to be in a genus by itself (Parr, 1946; Iwamoto and Stein, 1974). It has not been established that all of the species now included in the genus form a monophyletic group, and this can be discerned only through the study of all species of the group, rather than the study of representatives found in one area of the ocean at a time without consideration of the closely related forms. The unification of Nematonurus, Lionurus, Chalinura, and Albatrossia with Coryphaenoides has been followed here, since it was far beyond the scope of this work to examine all species assigned to Coryphaenoides.

Coryphaenoides rupestris is known from the North Atlantic at depths of 400 to 1200 meters (Marshall and Iwamoto, 1973). Most frequently caught in bottom trawls, it has also been captured in midwaters (Haedrich, 1974). The head is spherical and the snout is high and round. The scales of the

head are smaller than those covering the body and there are no ridges on the head or enlarged scales on the corners of the snout. The eyes are large, the barbel is moderate, and the mouth is moderate. It grows to a length of at least one meter. The flesh is soft and the skeleton is poorly ossified.

Coryphaenoides carapinus is a small species found at depths of 1400 to 2800 meters in the North Atlantic (Marshall and Iwamoto, 1973). The snout is the longest of any species of Coryphaenoides examined here, and is sharply pointed. There are pronounced ridges on the head without large scales. The eyes and barbel are both small and the mouth is moderately large.

Coryphaenoides armatus is one of the largest and most abundant macrourids. It has been caught from depths greater than 2200 meters in all oceans of the world except the Arctic (Iwamoto and Stein, 1974). The largest specimen reported measured 850mm total length. The snout is sharp and projects beyond the mouth in specimens smaller than 100mm total length, but as the animals get larger, the snout is more blunt and less prominent (Iwamoto and Stein, 1974). There are enlarged scales on the anterior of the snout. The eyes are moderate and a barbel is present. The mouth is moderately large. The ridges of the head are not greatly pronounced, and the body is stout and heavy with a well-ossified skeleton.

Coryphaenoides acrolepis is a large species known from

depths of 620 to 2200 meters in the Pacific. The eyes are large, there is a moderate barbel, and the mouth is large. The head is robust if compared to the body in small specimens (Iwamoto and Stein, 1974). Iwamoto and Stein (1974) report that the short snout is more slender and less bluntly pointed in specimens larger than 70mm head length, however the specimens examined in this study exhibit the opposite trend, similar to Coryphaenoides armatus, sharper snouts being found in smaller specimens. It grows to at least 783mm total length (Iwamoto and Stein, 1974). It is frequently caught in bottom trawls, but has also been caught in midwater nets (Iwamoto and Stein, 1974). It has been photographed at bait in the San Diego trough off the coast of California (Isaacs, 1969).

Coryphaenoides leptolepis has been caught at depths of 1900 to 3700 meters in the Atlantic and Pacific (Marshall and Iwamoto, 1973). The snout is low and blunt and the mouth is large. The eyes are small and the barbel short. It is similar to Coryphaenoides armatus in size and shape, being more laterally compressed and having less pronounced ridges on the head.

Coryphaenoides pectoralis is the largest known macrourid, reaching a length of at least 1500mm total length (Iwamoto and Stein, 1974). It is found in the North Pacific, with its center of distribution in the Bering Sea (Okamura, 1970a), at depths of 550 to 1200 meters. Eyes are moderate and the barbel is small. The body and head are laterally

compressed and there are no strong ridges on the side of the head. The mouth is large and there is a small snout. The musculature is soft and the skeleton is poorly ossified (Iwamoto and Stein, 1974). It may be a part-time inhabitant of midwaters (Iwamoto and Stein, 1974).

Macrourus berglax has been caught between 200 and 600 meters in the North Atlantic. It grows to at least 1 meter total length. The scales of the body have a large, sharp keel and the strong ridges of the head are covered with large, heavily keeled scales. The head is broad, with a large, high snout, and the trunk is long. The eyes are very large and the barbel is moderate. The mouth is moderate and is inferior to the snout.

Abyssicola macrochir is a large species with a long rostrum. It has been caught in waters near Japan at depths of 235 to 785 meters (Okamura, 1970a). The head is dorsoventrally depressed, with a high snout. Eyes are moderate and the mouth is large and inferior. This genus is often united with Coelorinchus, but its many differences with that otherwise unified genus have necessitated leaving it separate here.

Coelorinchus is a large genus, with some 65 species, divided into 5 fairly distinct subgenera (Gilbert and Hubbs, 1920). It is known from all oceans at depths less than 2000 meters. A light organ is present in all species, though

there is some variation within the genus in the morphology of the organ. All species have strong ridges on the side of the head ventral to the orbit, and continuing both anterior and posterior to the orbit. There is a long rostrum in all, and the mouths are small and inferior.

Coelorinchus coelorinchus carminatus is common in the western North Atlantic at depths of 100 to 900 meters (Marshall and Iwamoto, 1973). It is a small species with moderately large eyes and a relatively short and broad snout.

Coelorinchus chilensis is a small species from the eastern Pacific with immense eyes.

Coelorinchus longissimus has been caught at depths of 280 to 400 meters in the northwest Pacific (Okamura, 1970a). It grows to a length of at least 357mm total length. The head is large, with a long rostrum and a fairly large mouth.

Coelorinchus occa is known from the Gulf of Mexico and western North Atlantic at depths of 460 to 2200 meters. It is one of the largest species of Coelorinchus, growing to at least 500mm total length. The rostrum is long and the scales of the infraorbital ridge are very large.

Coelorinchus jordani is a small species with a strongly compressed body and anteriorly depressed head. The rostrum is short and broad, and the mouth is small.

Coelorinchus innotabilis is a small species from the Antarctic and eastern Pacific. The body is nearly cylindrical

and the rostrum is long and pointed.

Coelorinchus japonicus is a large species from Japanese waters at depths of 300 to 600 meters, with larger specimens occurring at greater depths (Okamura, 1970a). It has a long rostrum and a fairly large mouth.

The subfamily Trachyrincinae consists of six species of the genus Trachyrincus, distinct from the rest of the family in having a small true caudal skeleton (Marshall and Iwamoto, 1973). The overall shape is reminiscent of Coelorinchus, with a long rostrum and inferior mouth, but there are a number of differences between them that make Trachyrincus very distinctive within the family. Trachyrincus helolepis is a moderate size species from the eastern Pacific. The head is depressed dorsoventrally, there is no barbel or luminous tissue, and the eyes are large and oval.

## II. Cranium

The cranium of macrourids is elongate and dorsoventrally depressed. The greatest amount of variation within the family in the cranium is in the size and shape of the nasal bones. The nasals are paired bones, anterior to the frontals and dorsal to the premaxilla and ethmoid.

The least specialized condition of the nasals is found in Macruronus novaezelandiae (figures 13 and 14), Steindachneria argentea (figures 15 and 16), and Bathygadus macrops (figures 17 and 18). In these species the nasals barely touch each

Figure 13. Dorsal view of the skull of Macruronus  
novaezelandiae, MCZ 48944, 59 mm HL.

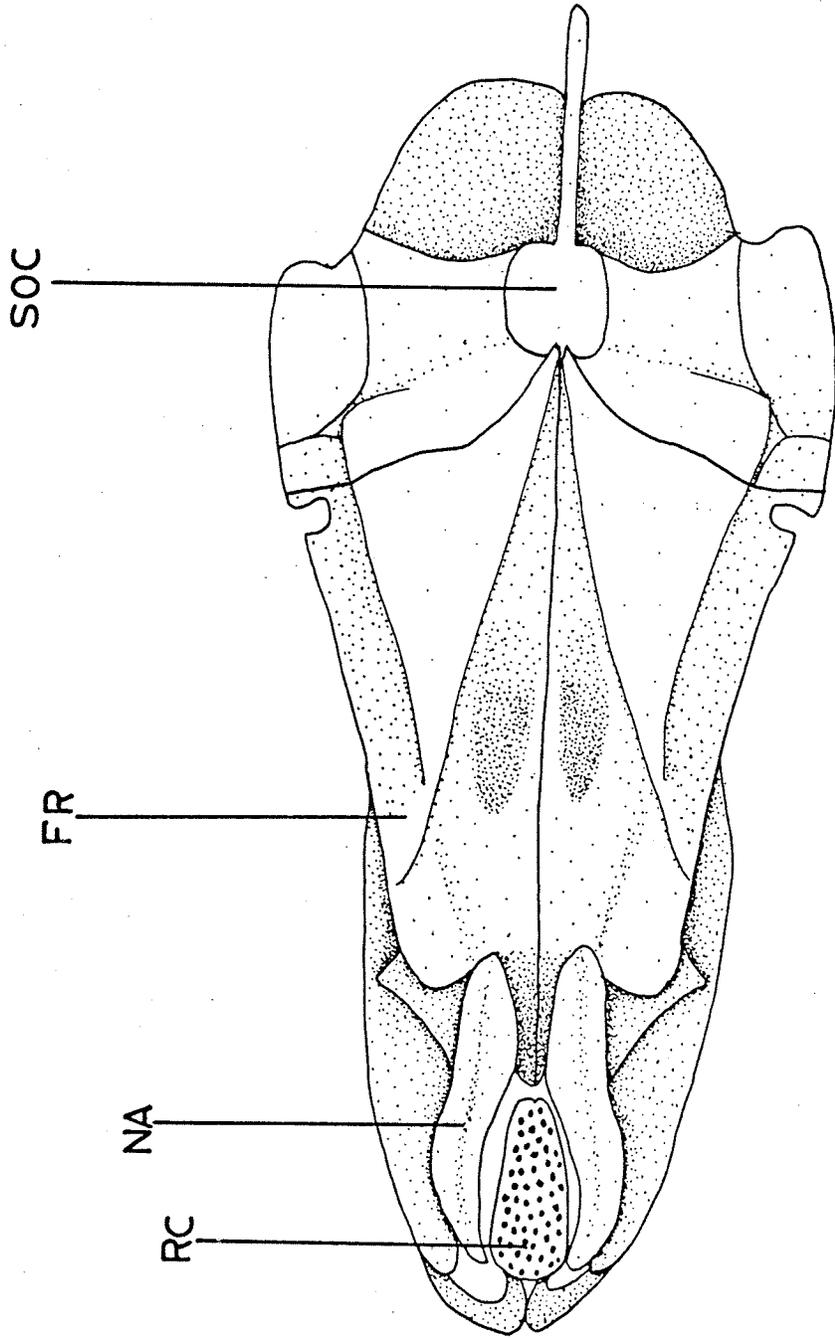


Figure 14. Lateral view of the skull of Macruronus  
novaezelandiae, MCZ 48944, 59 mm HL.

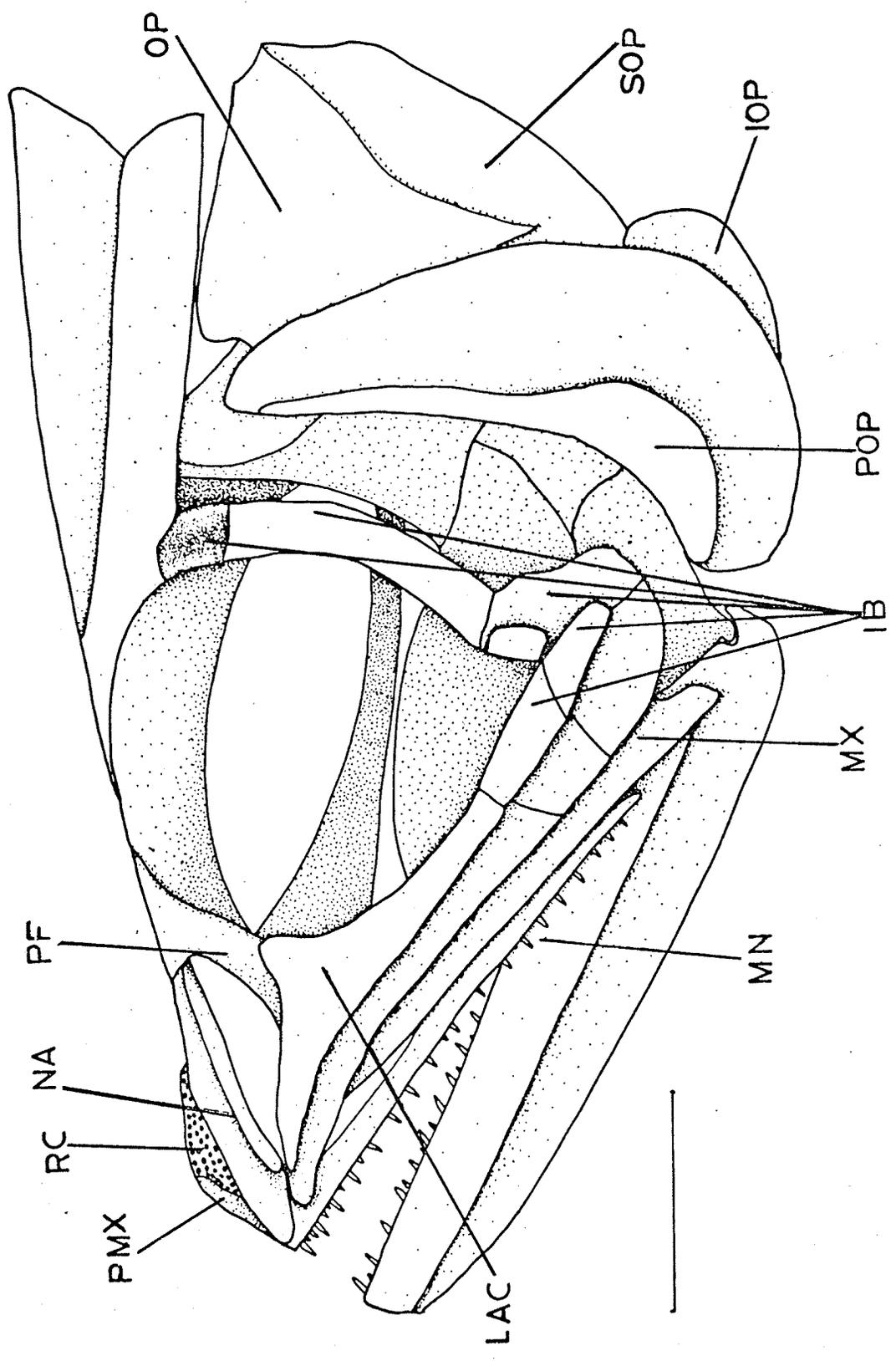


Figure 15. Dorsal view of the skull of Steindachneria  
argentea, USNM 188852, 43 mm HL.

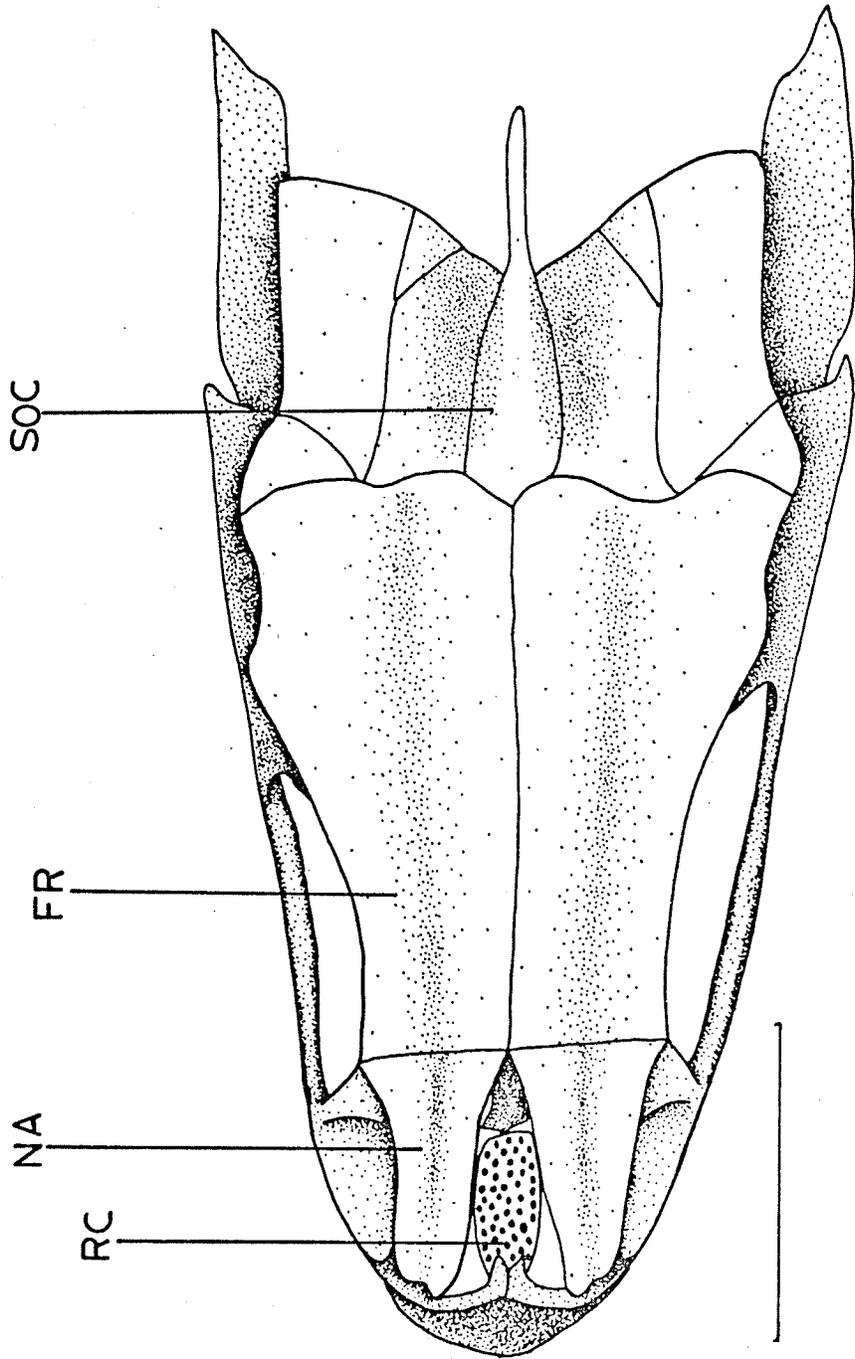


Figure 16. Lateral view of the skull of Steindachneria  
argentea, USNM 188852, 43 mm HL.

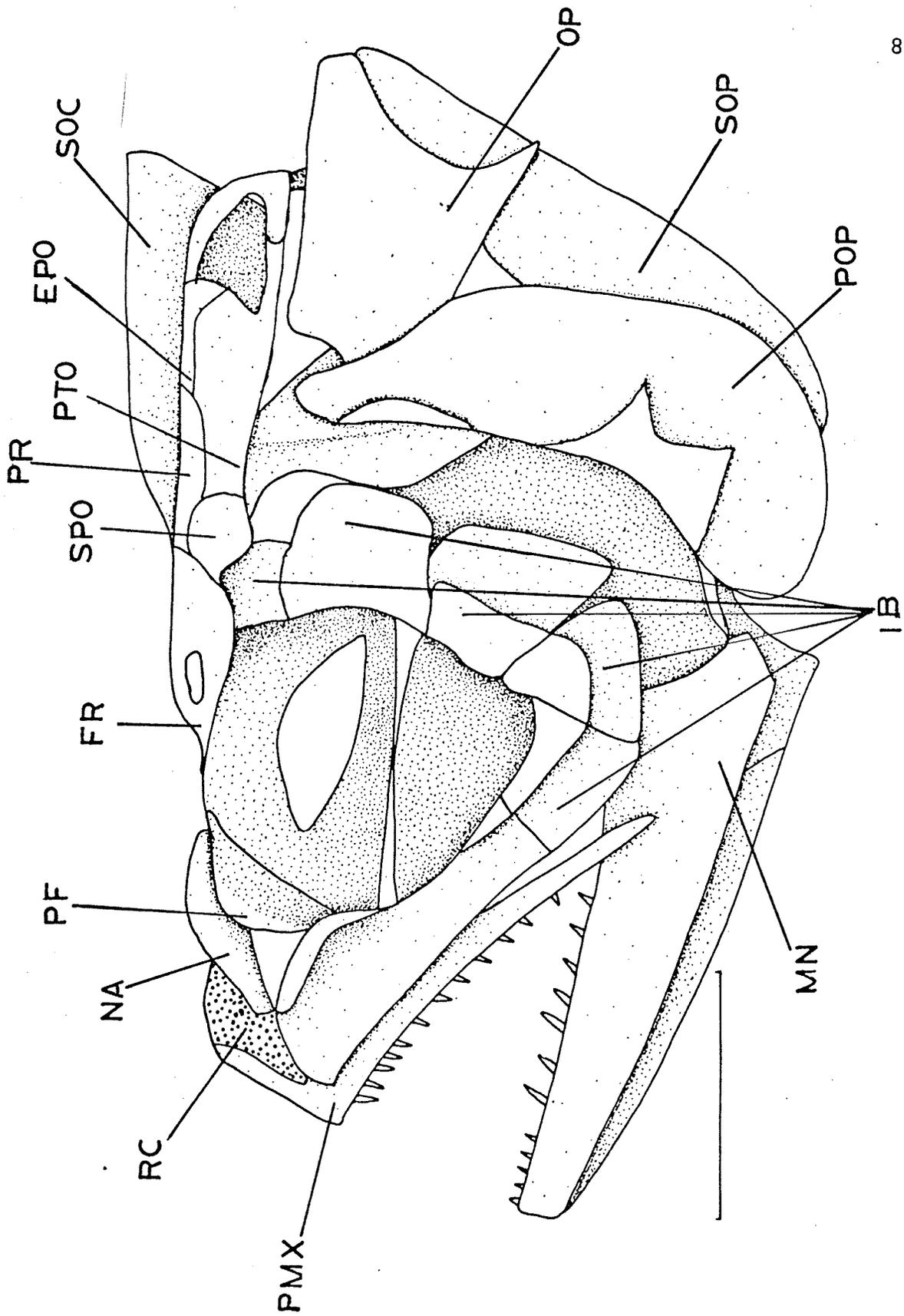


Figure 17. Dorsal view of the skull of Bathygadus  
macrops, MCZ 51168, 79 mm HL.

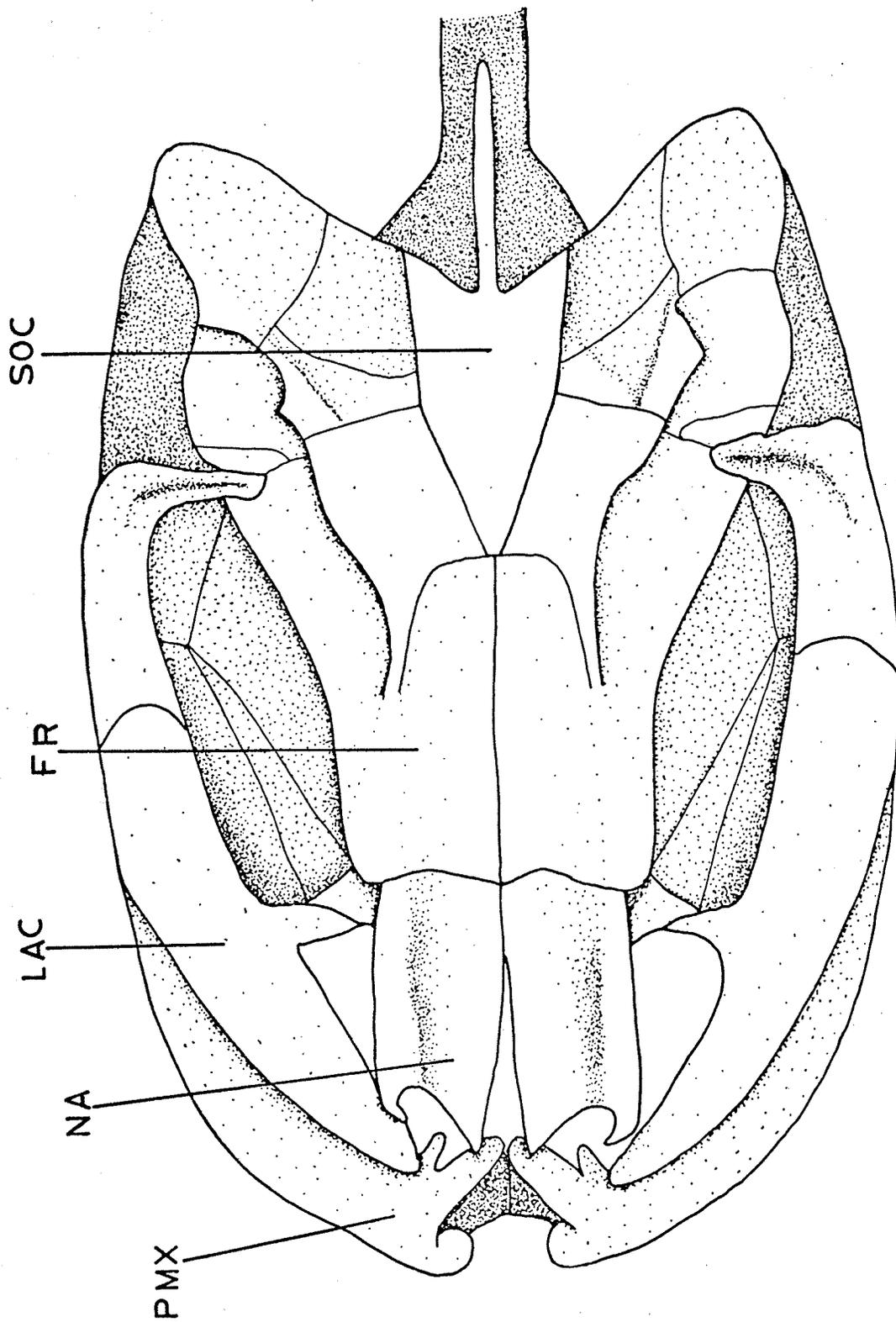
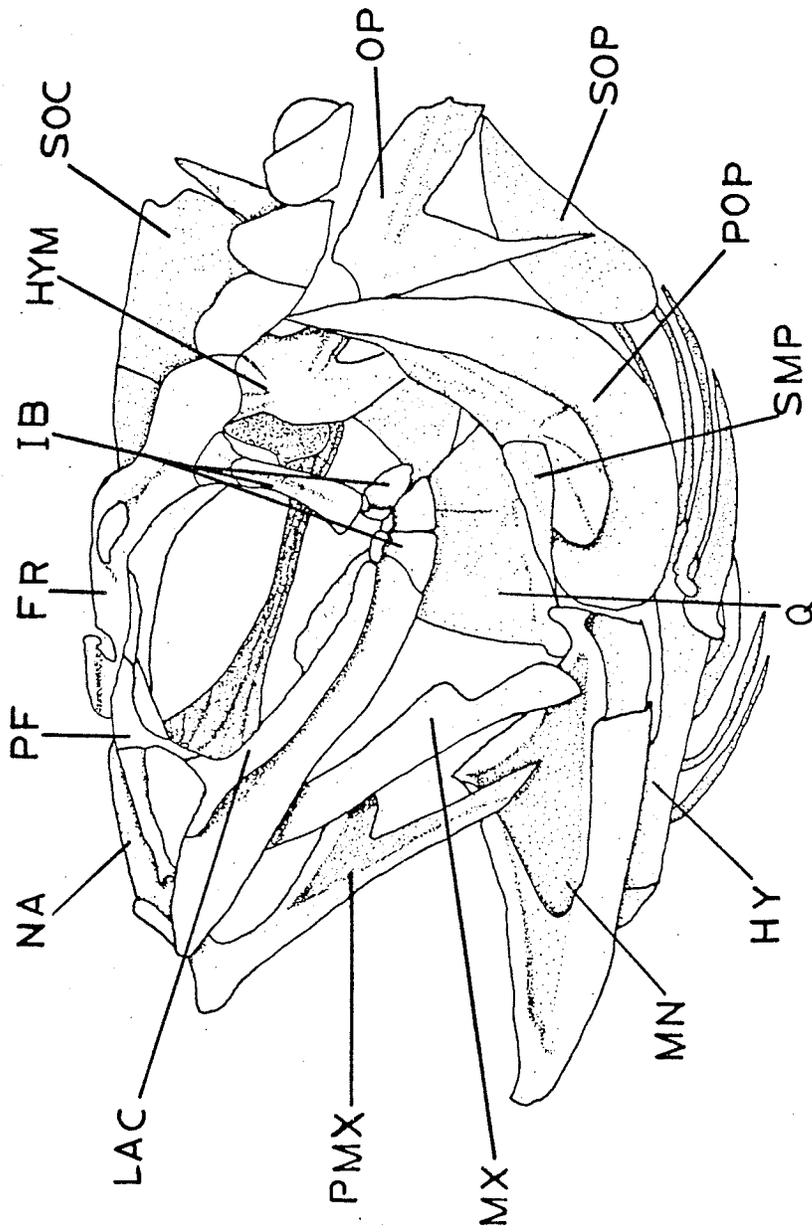


Figure 18. Lateral view of the skull of Bathygadus  
macrops, composite of UMML 15193, 68 mm HL, and MCZ  
51168, 79 mm HL.



other along the midline at the point where they meet the frontals and are separate from each other distally. The rostral cartilage enters the dorsal profile of the head when the mouth is closed, and the nasals curve around it.

In Macruronus novaezelandiae the nasals are slender rectangles with round anterior edges. Those of Steindachneria argentea are shorter and broader and the anterior edge has two small rounded corners. In Bathygadus macrops they are even shorter and there are two distinct corners anteriorly.

Lepidorhynchus denticulatus (figure 19) has a short rostrum supported by small, thin nasals that meet along the midline for the posterior half of their length. The anterior corners are developed into short, acute processes.

Malacocephalus occidentalis has nasals that are united along the midline for their entire length (figures 20 and 21). The anterior corners are developed into distinct processes with a deep notch between them where a lateral line canal passes. The medial processes are thin and form an acuminate tip; the lateral processes are small and thin. Along the midline there is a thin dorsal keel for the posterior half of the length of the nasals which is continuous posteriorly with a smaller keel of the frontals.

Nezumia bairdii has strong, stout nasals with wide medial processes and strong lateral processes that curve ventrally around the anterior edge of the nasal capsule (figures 22 and

Figure 19. Lateral view of the skull of Lepidorhynchus  
denticulatus, MCZ 51515, 57 mm HL.

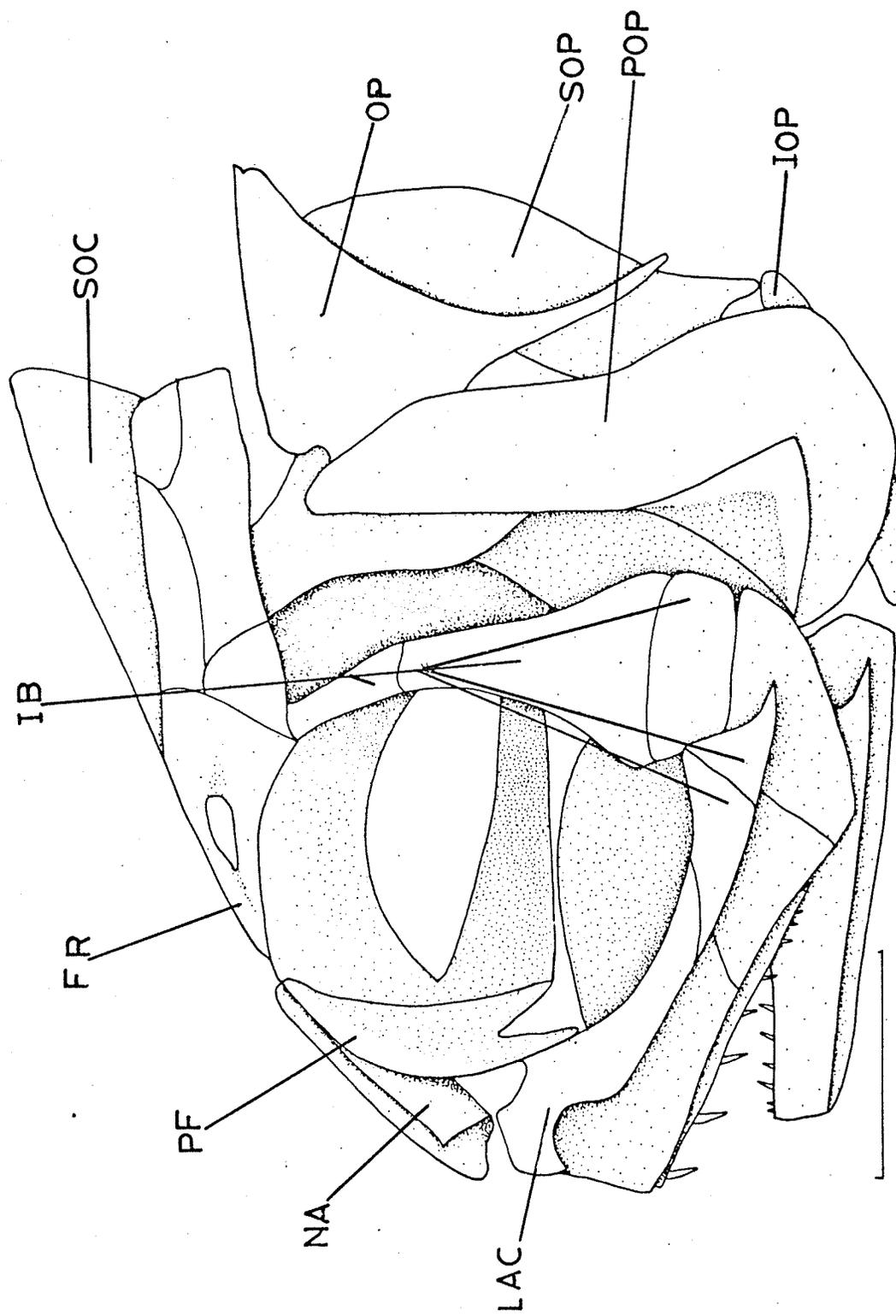


Figure 20. Dorsal view of the skull of Malacocephalus  
occidentalis, MCZ 51167, 68 mm HL.

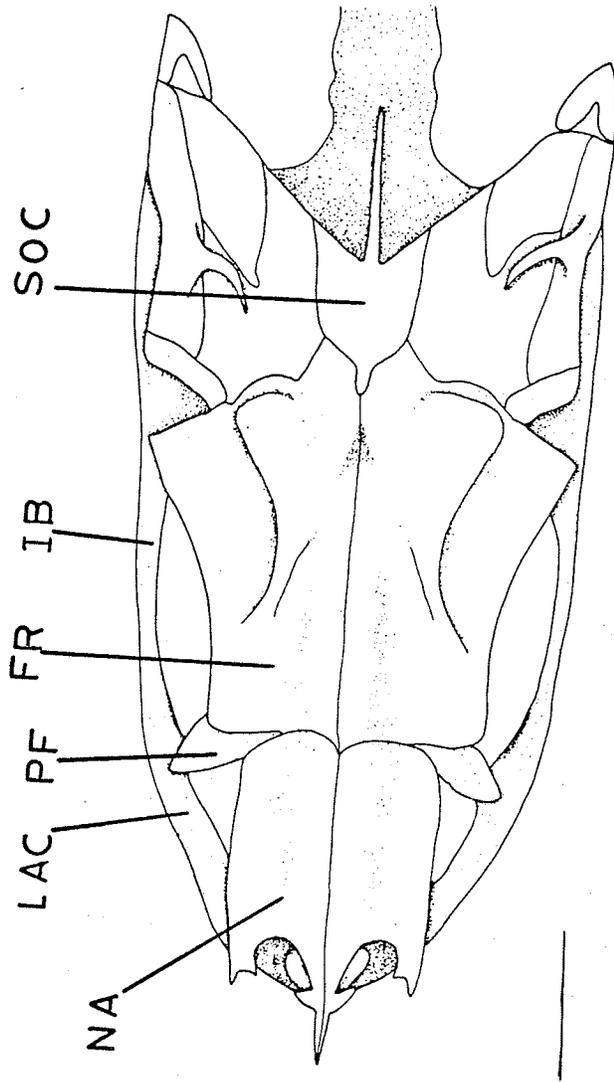


Figure 21. Lateral view of the skull of Malacocephalus  
occidentalis, composite of UMML 25600, 51 mm HL, and  
MCZ 51167, 68 mm HL.

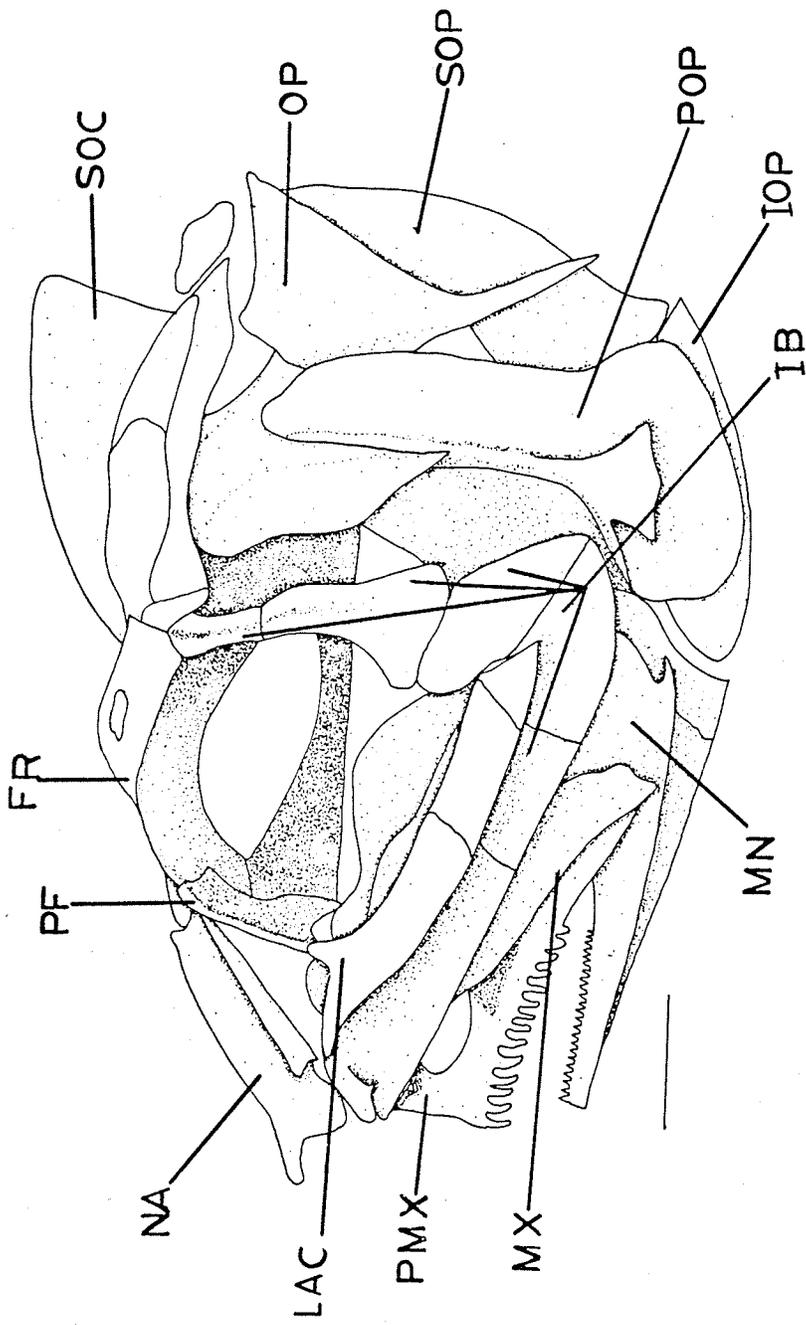


Figure 22. Dorsal view of the skull of Nezumia  
bairdii, MCZ 51466, 61 mm HL.

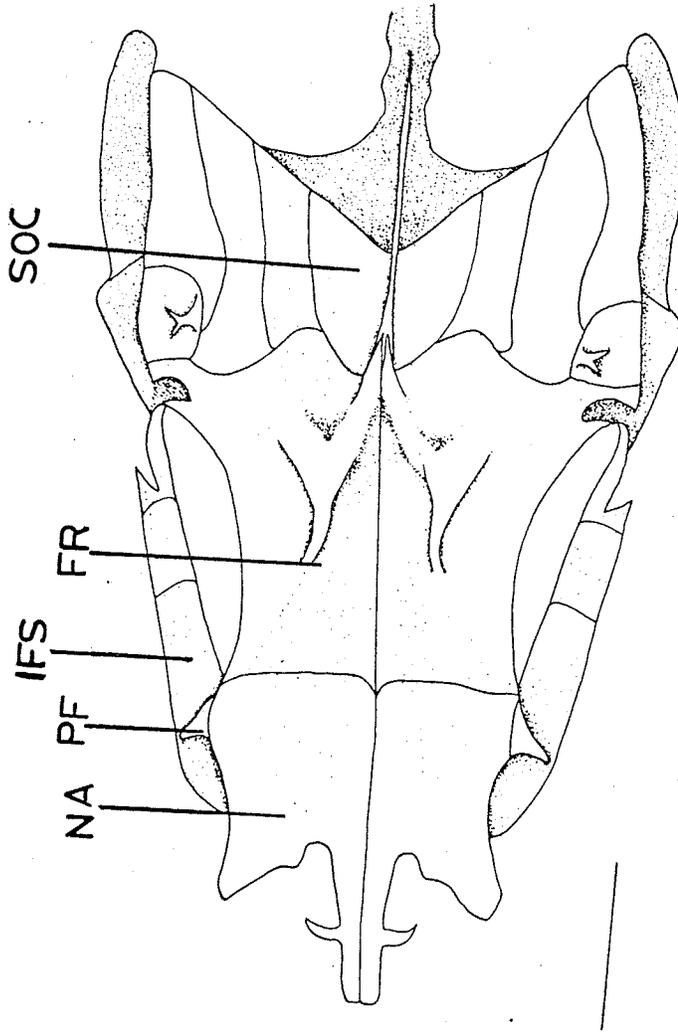
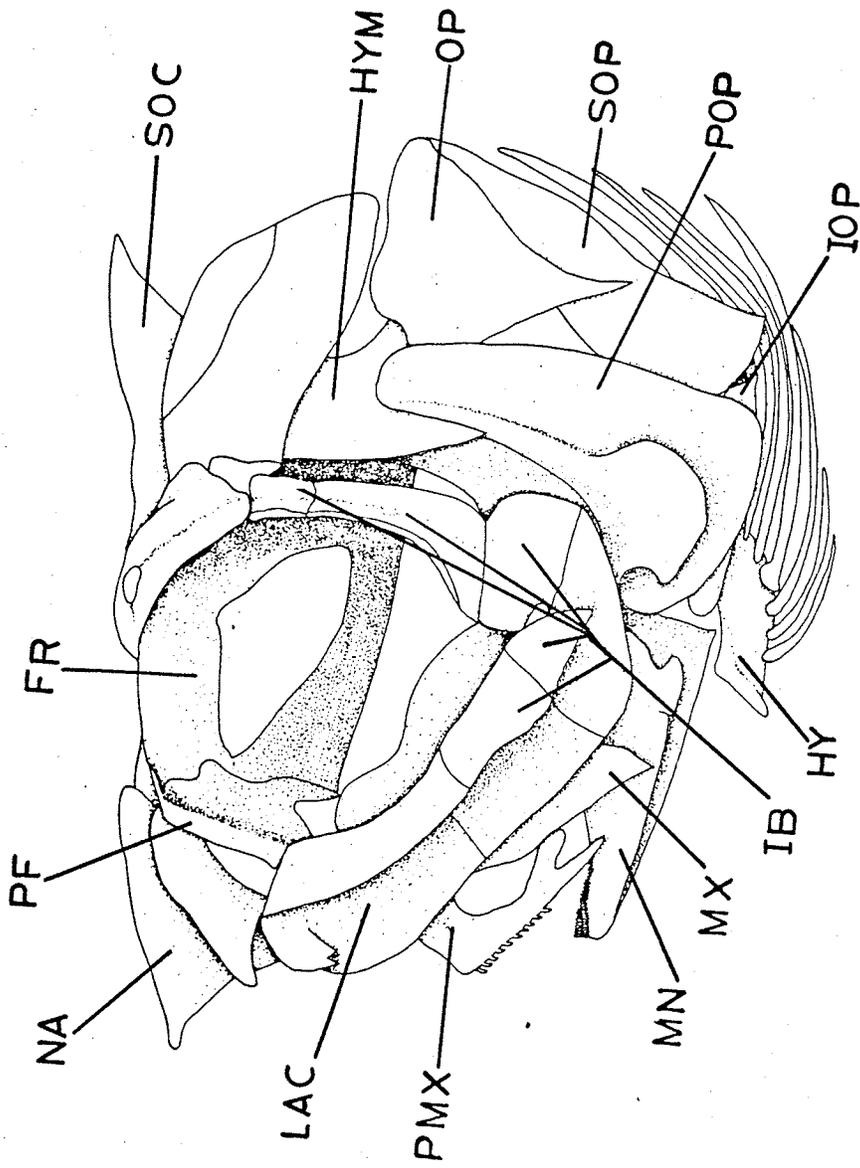


Figure 23. Lateral view of the skull of Nezumia  
bairdii, MCZ 51466, 61 mm HL.



23).

The nasals of Mataeocephalus acipenserinus are very long with long, slender medial processes (figures 24 and 25). The distal ends of the medial processes are separated from each other and each bears a cap-like scale. The lateral processes are short and thin and do not extend anteriorly to the nostril.

Coryphaenoides rupestris has a poorly ossified skull with large spaces filled with cavernous lateral line canals (figures 26 and 27). The nasals are broad posteriorly and have a high median keel. The lateral edge curves ventrally around the nasal capsule and does not enter into the lateral margin of the rostrum.

Coryphaenoides carapinus has longer nasals than any of the other species of Coryphaenoides examined. The bones are thin and are usually crushed when the fish are caught. The medial processes are broad and there is a pronounced dorsal keel (figures 28 and 29). The lateral edge is similar to that of Coryphaenoides rupestris, with no extension anterior to the nasal capsule. The notch between the medial and lateral processes is about one third the length of the nasal.

Coryphaenoides armatus has short, strong nasals with a shallow dorsal keel (figures 30 and 31). The medial processes are stout and the lateral processes are wide. Coryphaenoides acrolepis is similar to C. armatus, except that the nasals are broader posteriorly (figures 32 and 33). In both species the rostrum is more pointed in smaller individuals than in

Figure 24. Dorsal view of the skull of Mataeocephalus  
acipenserinus, USNM 126542, 50 mm HL.

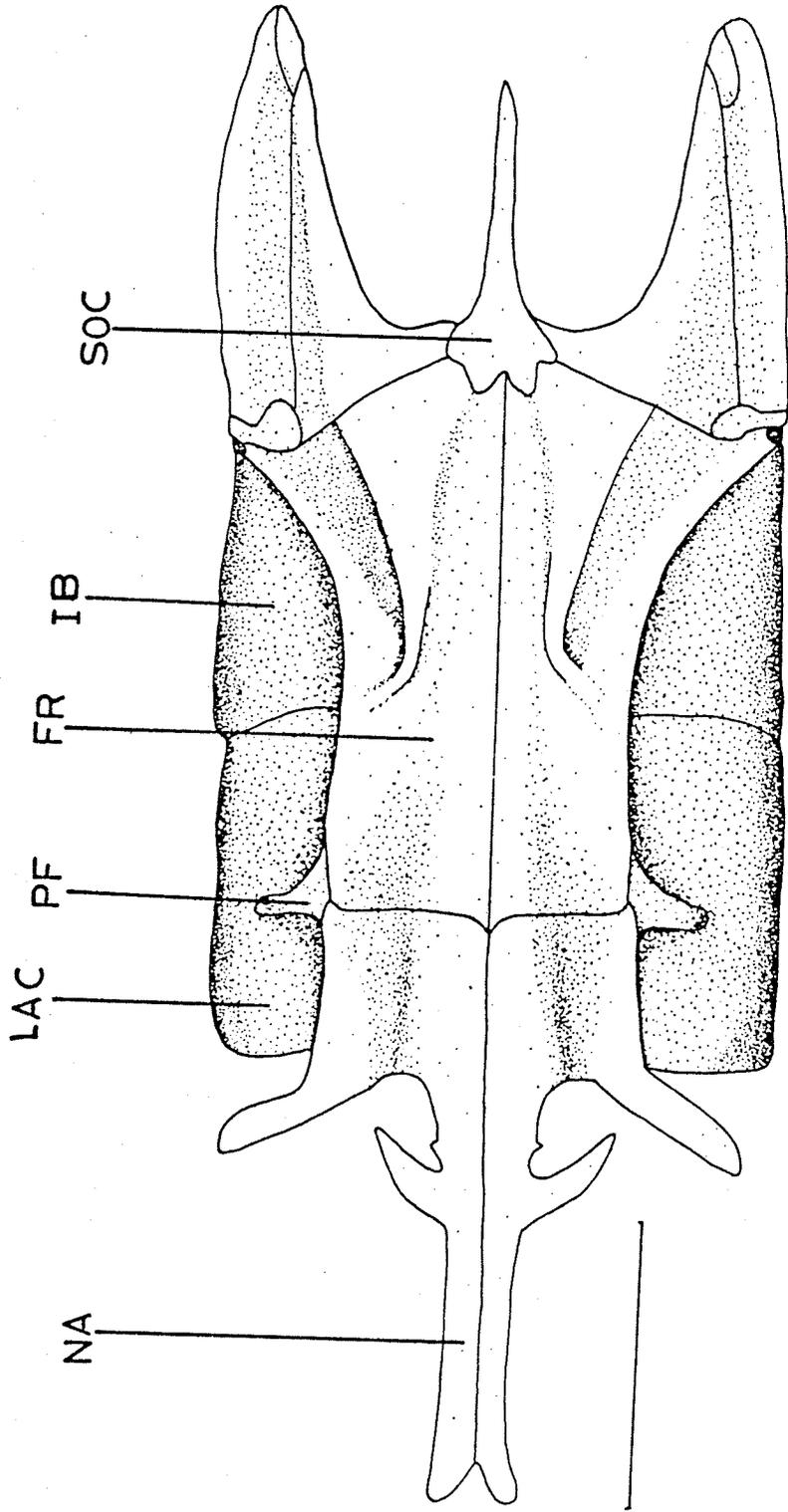


Figure 25. Lateral view of the skull of Mataeocephalus  
acipenserinus, USNM 126542, 50 mm HL.

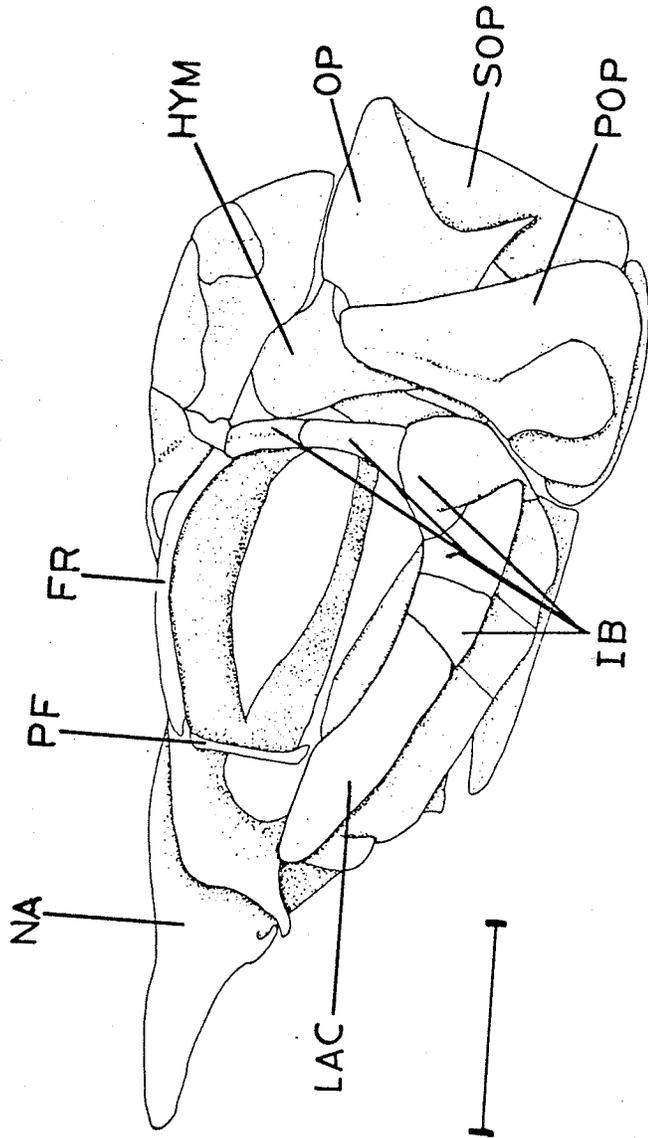


Figure 26. Dorsal view of the skull of Coryphaenoides  
rupestris. MCZ 51462, 142 mm HL.

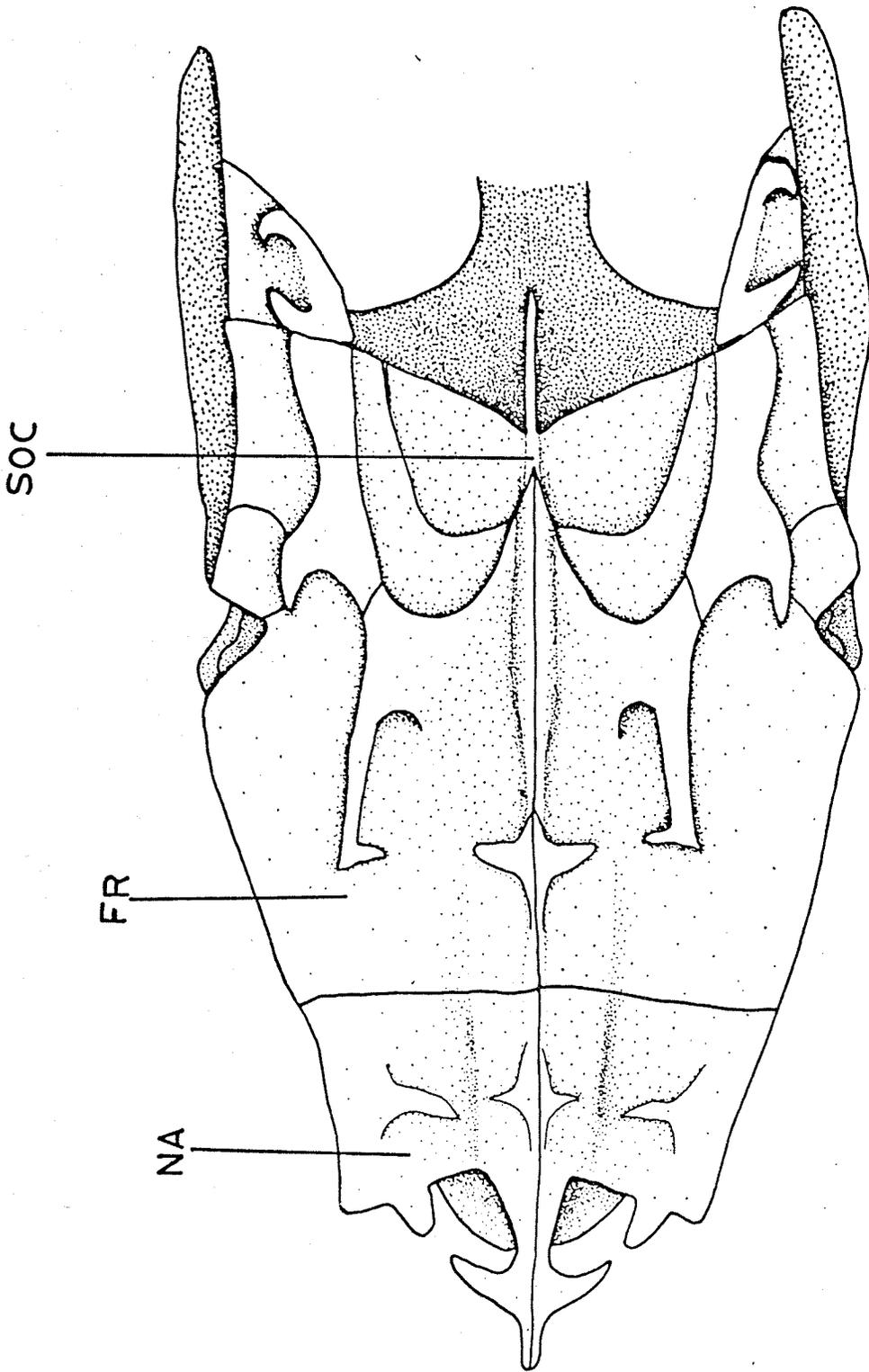


Figure 27. Lateral view of the skull of Coryphaenoides  
rupsestris, MCZ 51462, 142 mm HL.

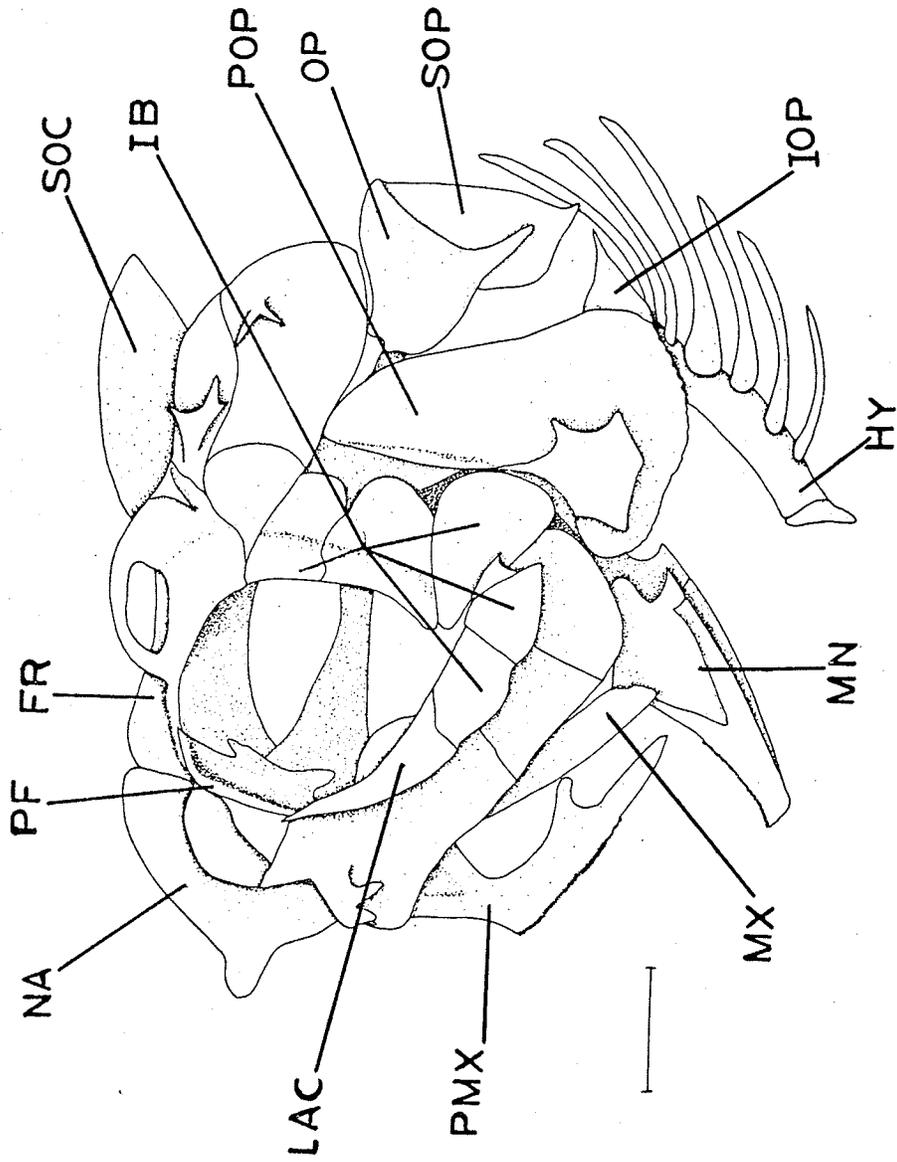


Figure 28. Dorsal view of the skull of Coryphaenoides  
carapinus, MCZ 51178, 52 mm HL.

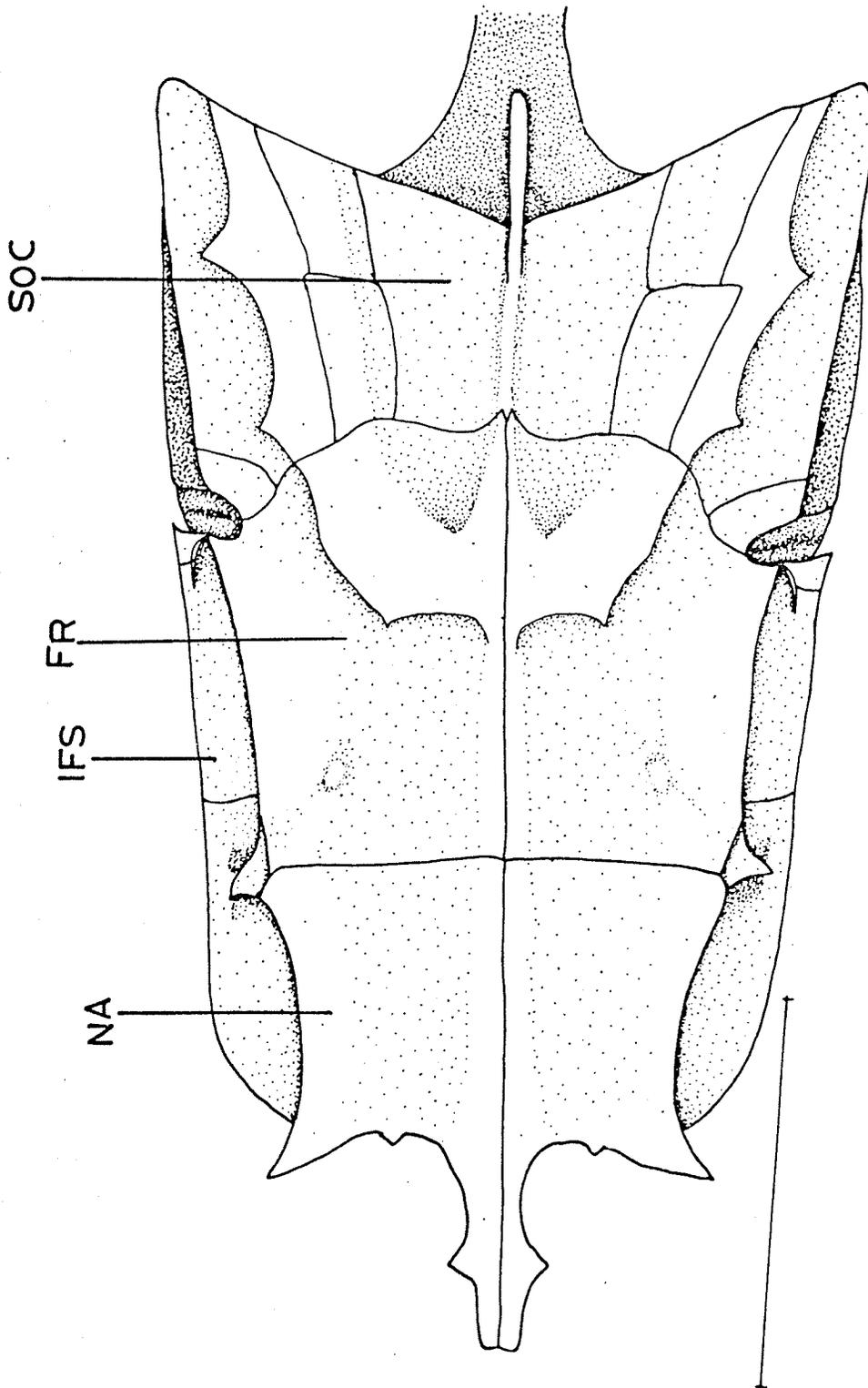


Figure 29. Lateral view of the skull of Coryphaenoides  
carapinus, MCZ 51178, 52 mm HL.

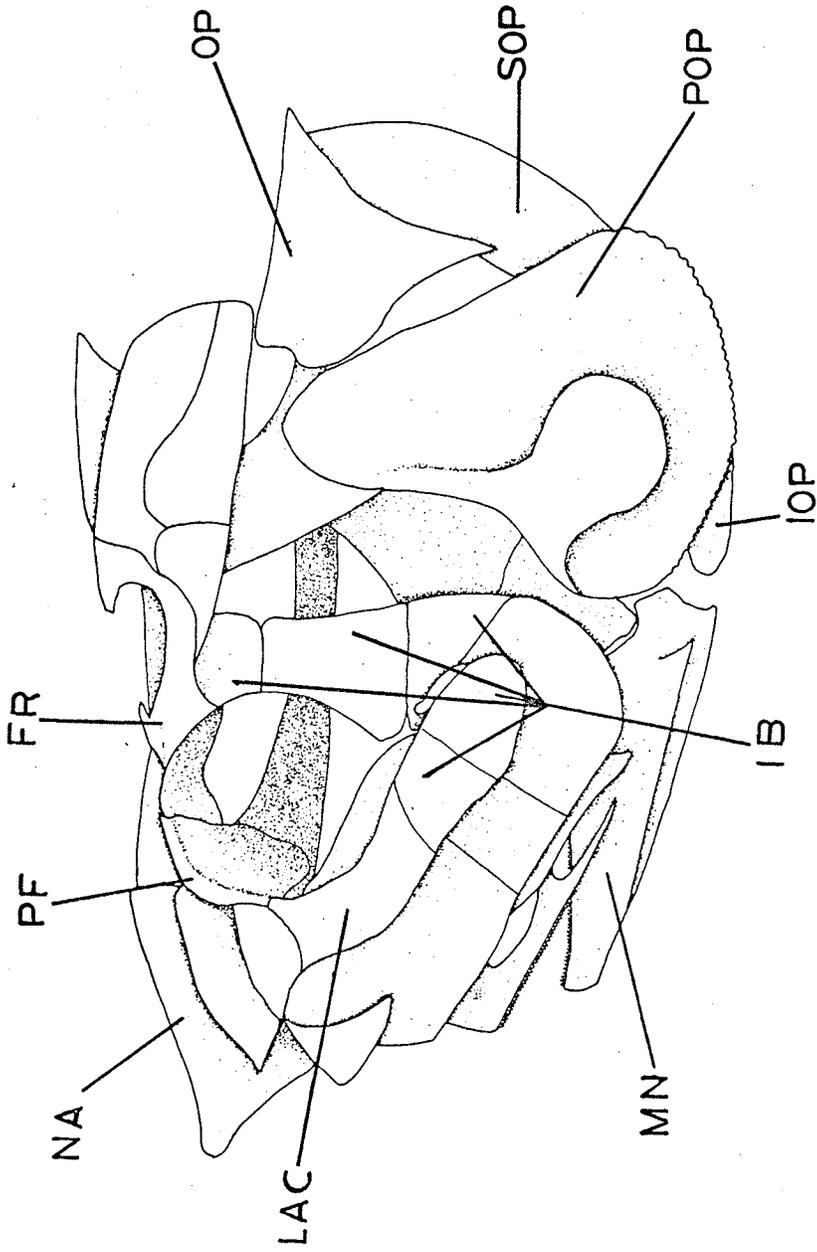


Figure 30. Dorsal view of the skull of Coryphaenoides armatus, MCZ 51464, 99 mm HL.

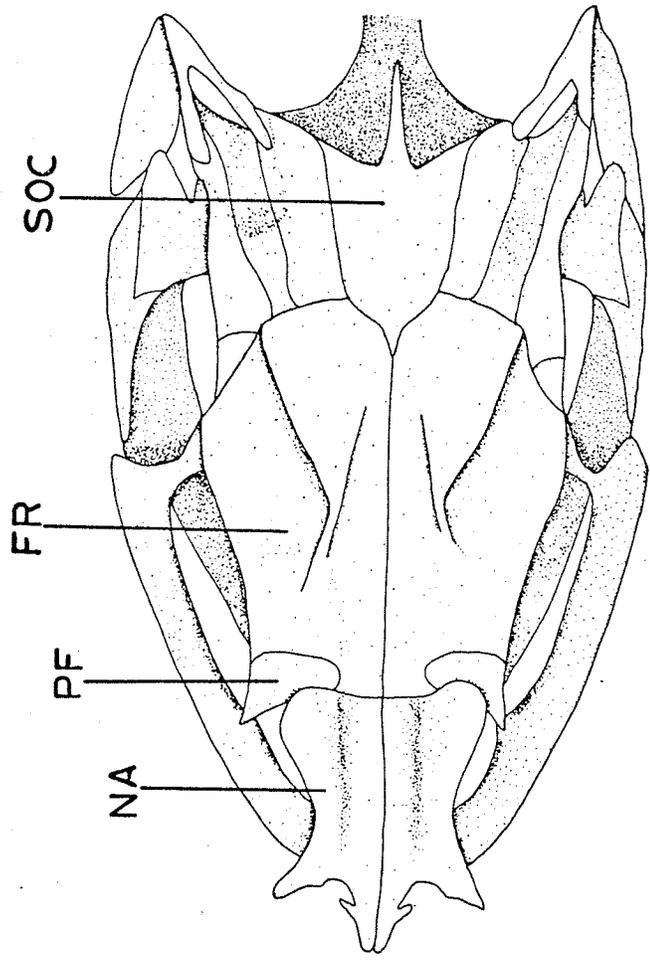


Figure 31. Lateral view of the skull of Coryphaenoides armatus, MCZ 51464, 99 mm HL.

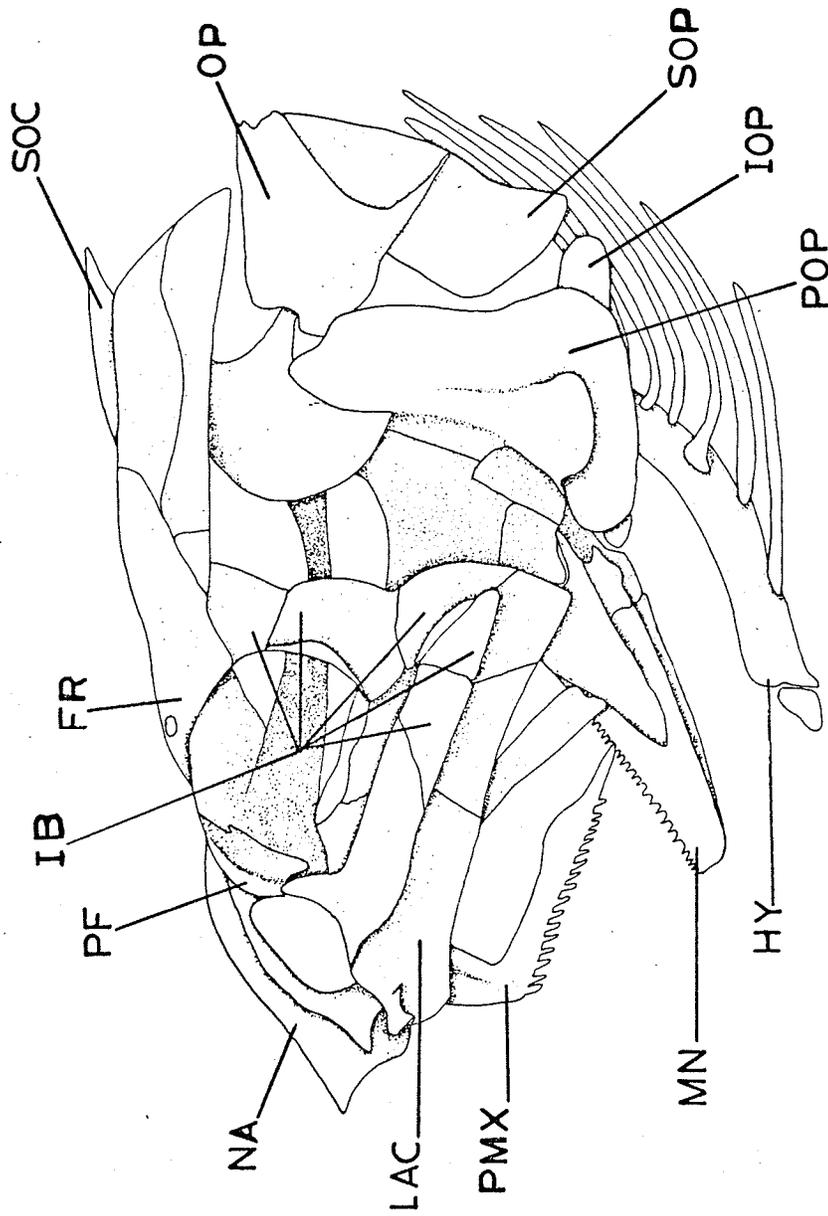


Figure 32. Dorsal view of the skull of Coryphaenoides  
acrolepis, MCZ 51926, 156 mm HL.

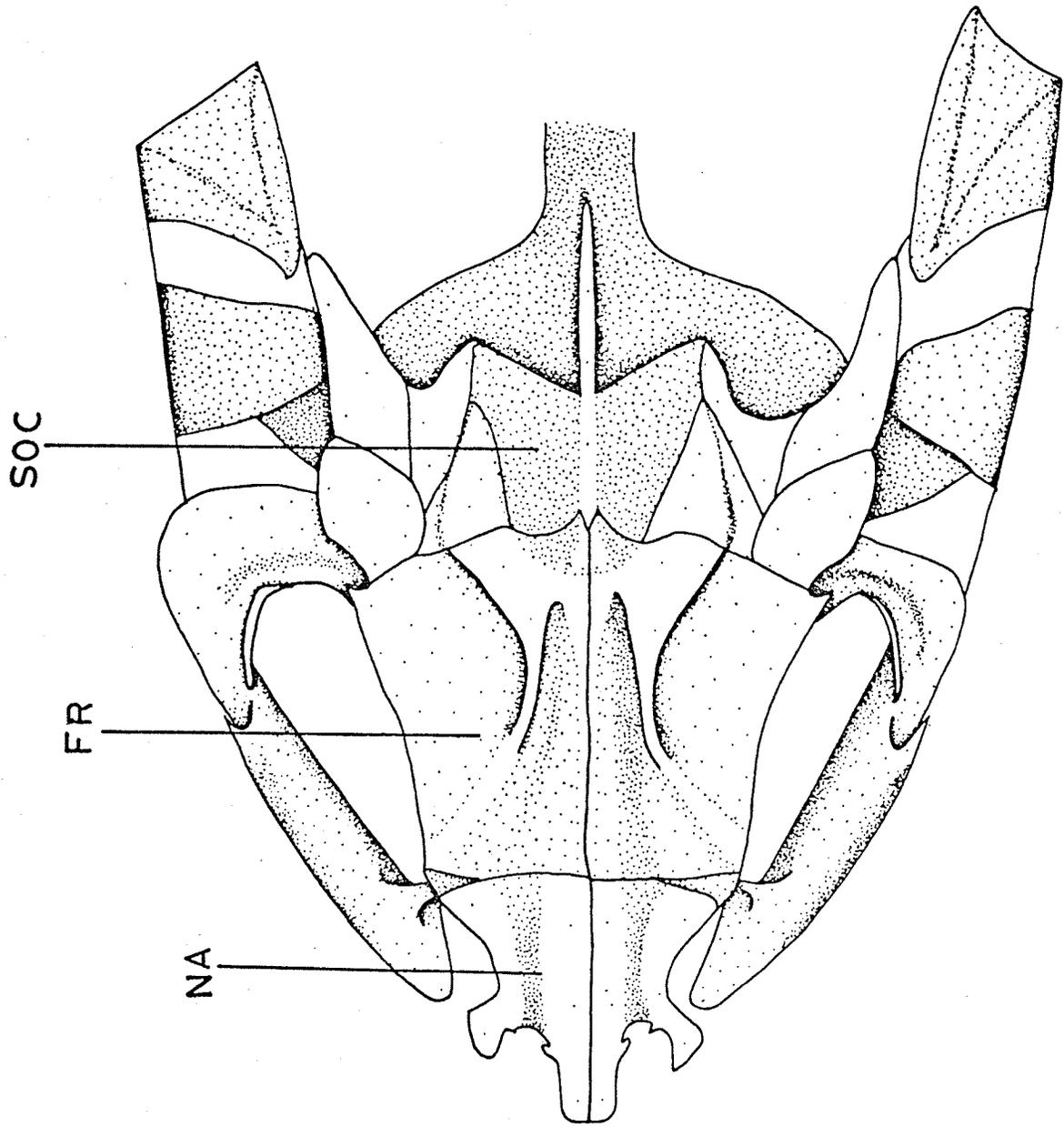
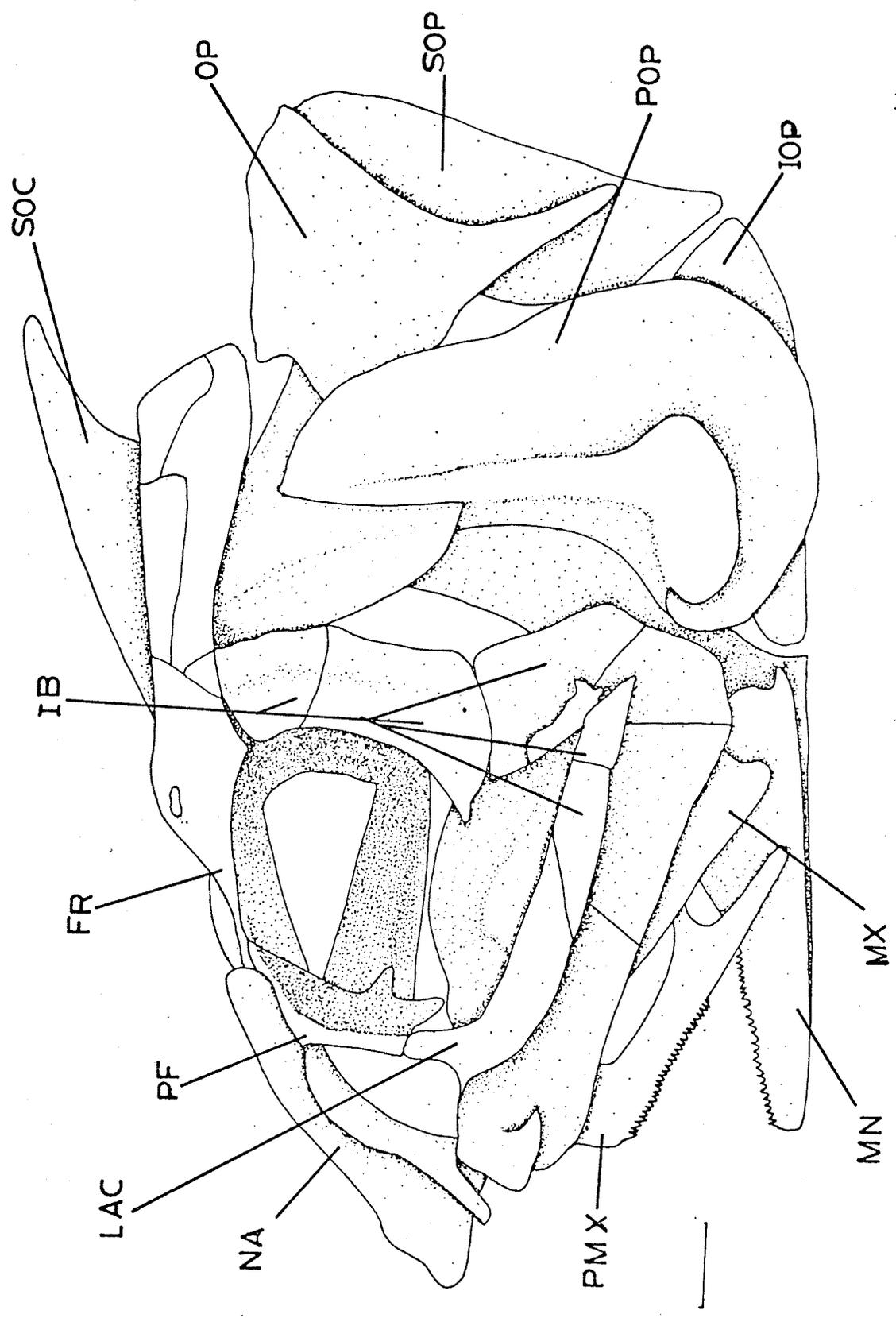


Figure 33. Lateral view of the skull of Coryphaenoides  
acrolepis, MCZ 51926, 156 mm HL.

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larger ones (see page 73 ).

Coryphaenoides leptolepis has thin nasals with small anterior processes and a shallow notch between them (figures 34 and 35). Coryphaenoides pectoralis also has small nasals with short anterior processes (figure 36).

Macrourus berglax has stout nasals of thick bone, with well developed medial and lateral processes (figures 2 and 37). The nasals of Abyssicola macrochir have a long, narrow medial process and small lateral processes. There is a very high dorsal keel along the posterior half of the nasals (figures 38 and 39).

Coelorinchus coelorinchus carminatus has nasals with strong, straight medial processes and flat lateral processes that border the lateral margin of the rostrum anterior to the nasal capsule for a short distance (figures 40 and 41). The nasals of Coelorinchus chilensis are short, with widely separated, short anterior processes (figures 42 and 43).

Coelorinchus longissimus has very long nasals with wide medial processes and long, anteriorly pointed lateral processes. The medial processes are widest a short distance posterior to the tip, so that they border the lateral margin of the rostrum for about the anterior one third of its length, and the lateral processes fill the posterior one third of the margin of the rostrum anterior to nasal capsule (figures 44 and 45).

Figure 34. Dorsal view of the skull of Coryphaenoides  
leptolepis, MCZ 51465, 98 mm HL.

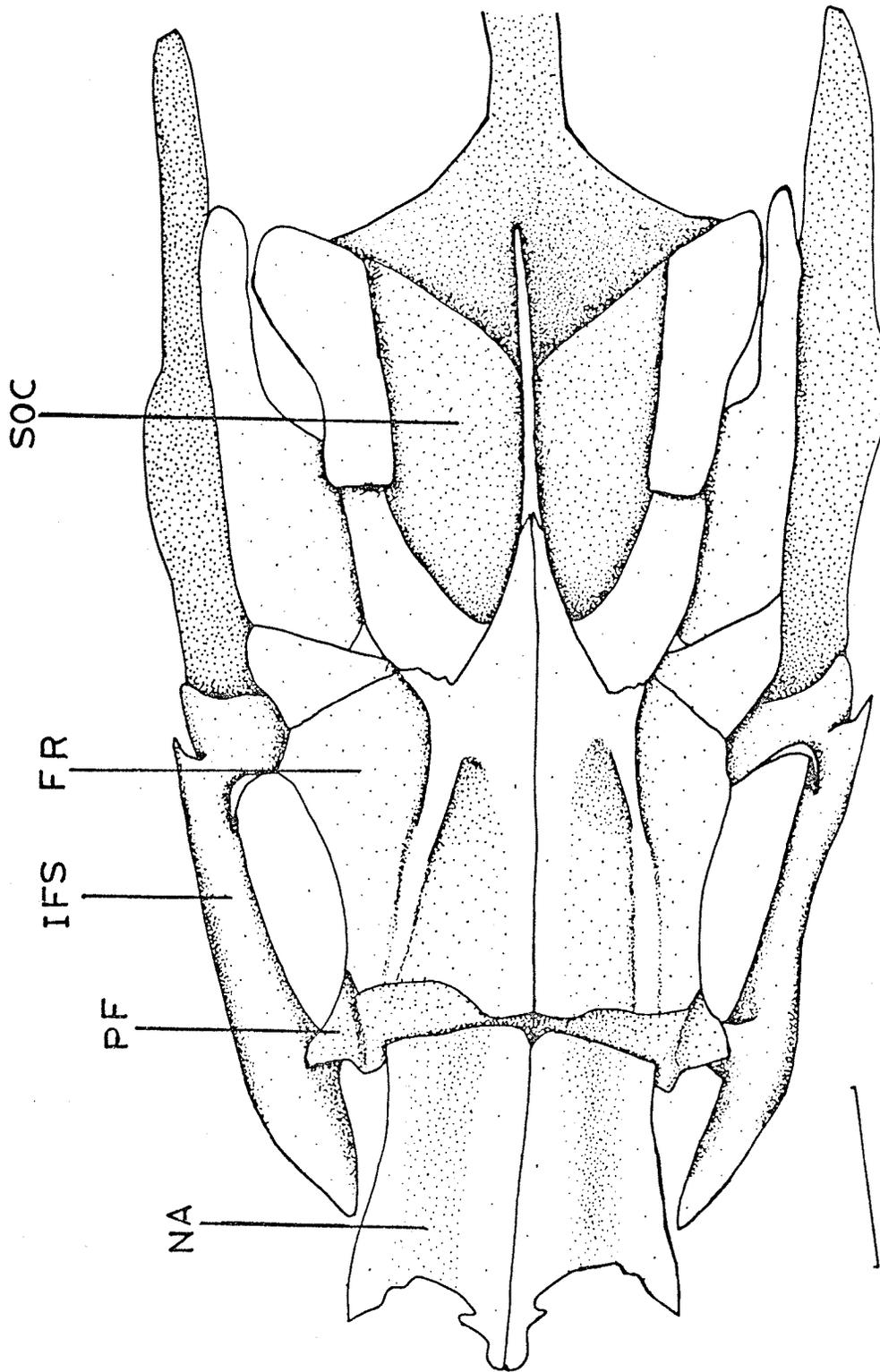


Figure 35. Lateral view of the skull of Coryphaenoides  
leptolepis, MCZ 51465, 98 mm HL.

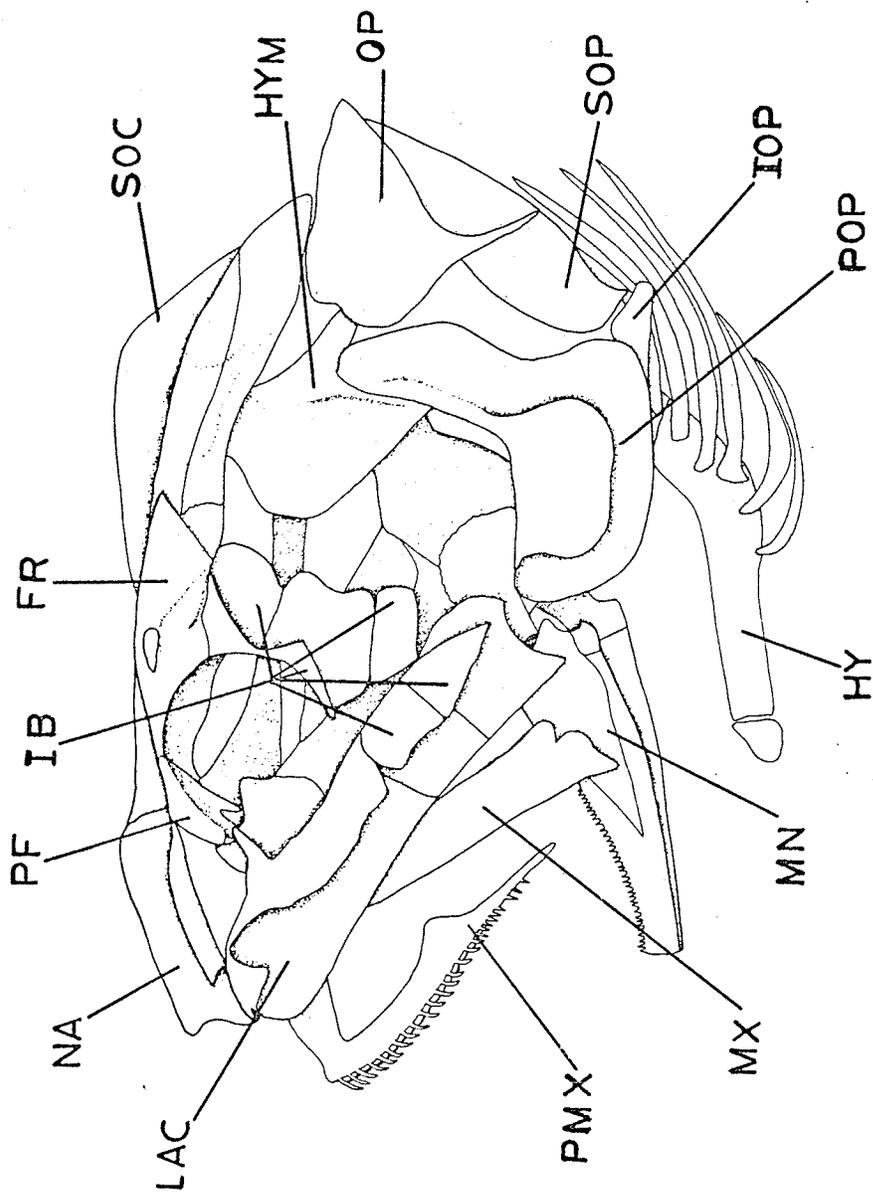


Figure 36. Lateral view of the skull of Coryphaenoides  
pectoralis, MCZ 51929, 110 mm HL.

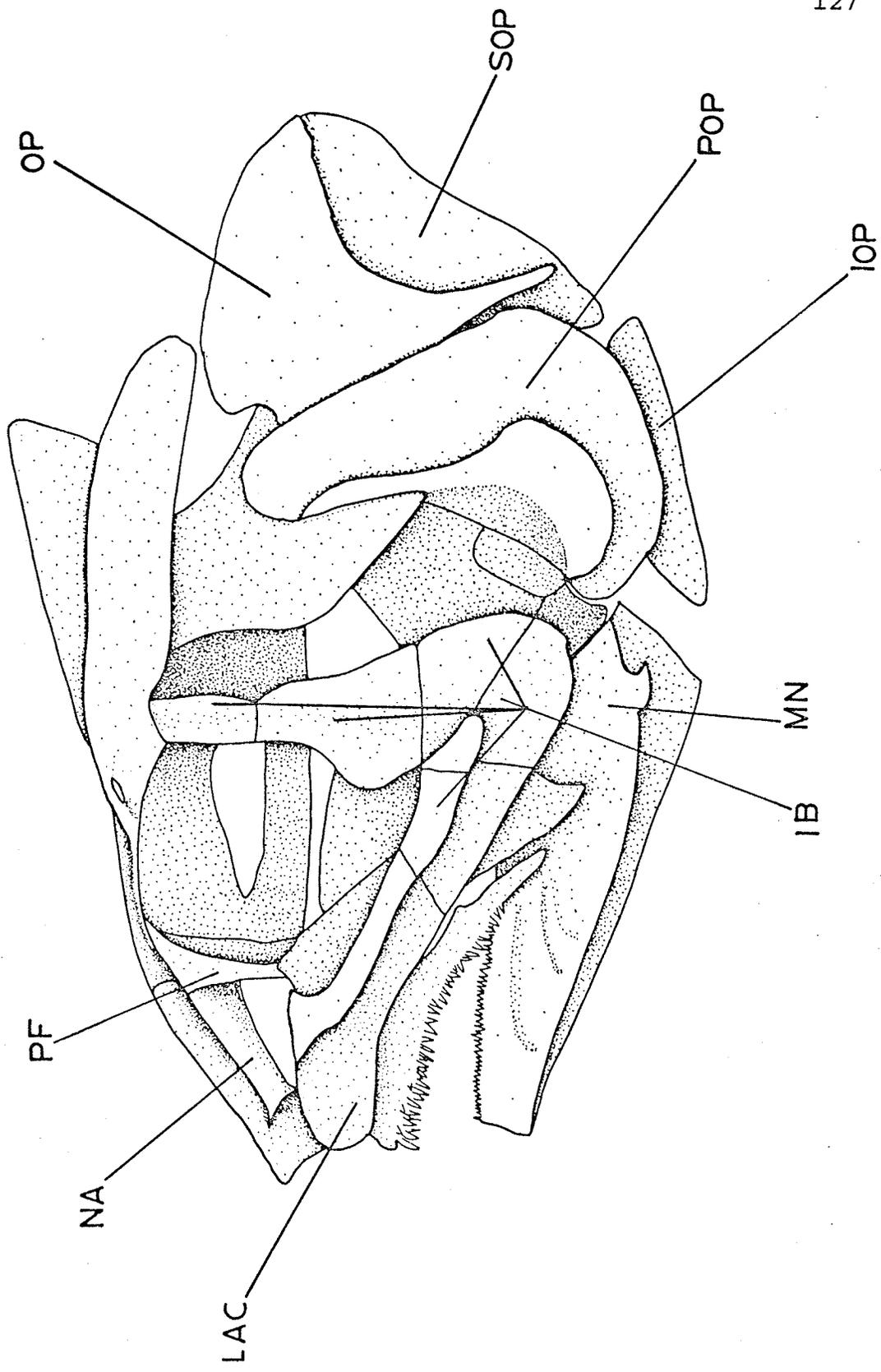


Figure 37. Dorsal view of the skull of Macrourus  
berglax, MCZ 51463, 145 mm HL.

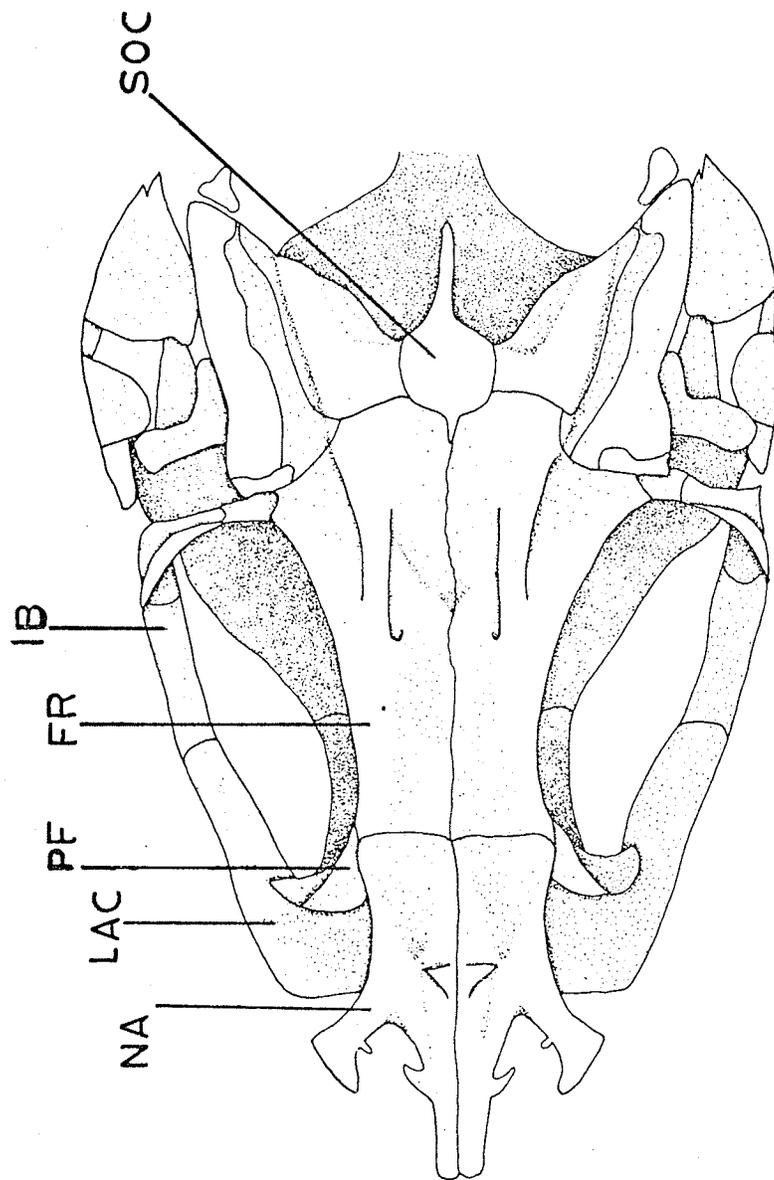


Figure 38. Dorsal view of the skull of Abyssicola  
macrochir, USNM 77248, 75 mm HL.

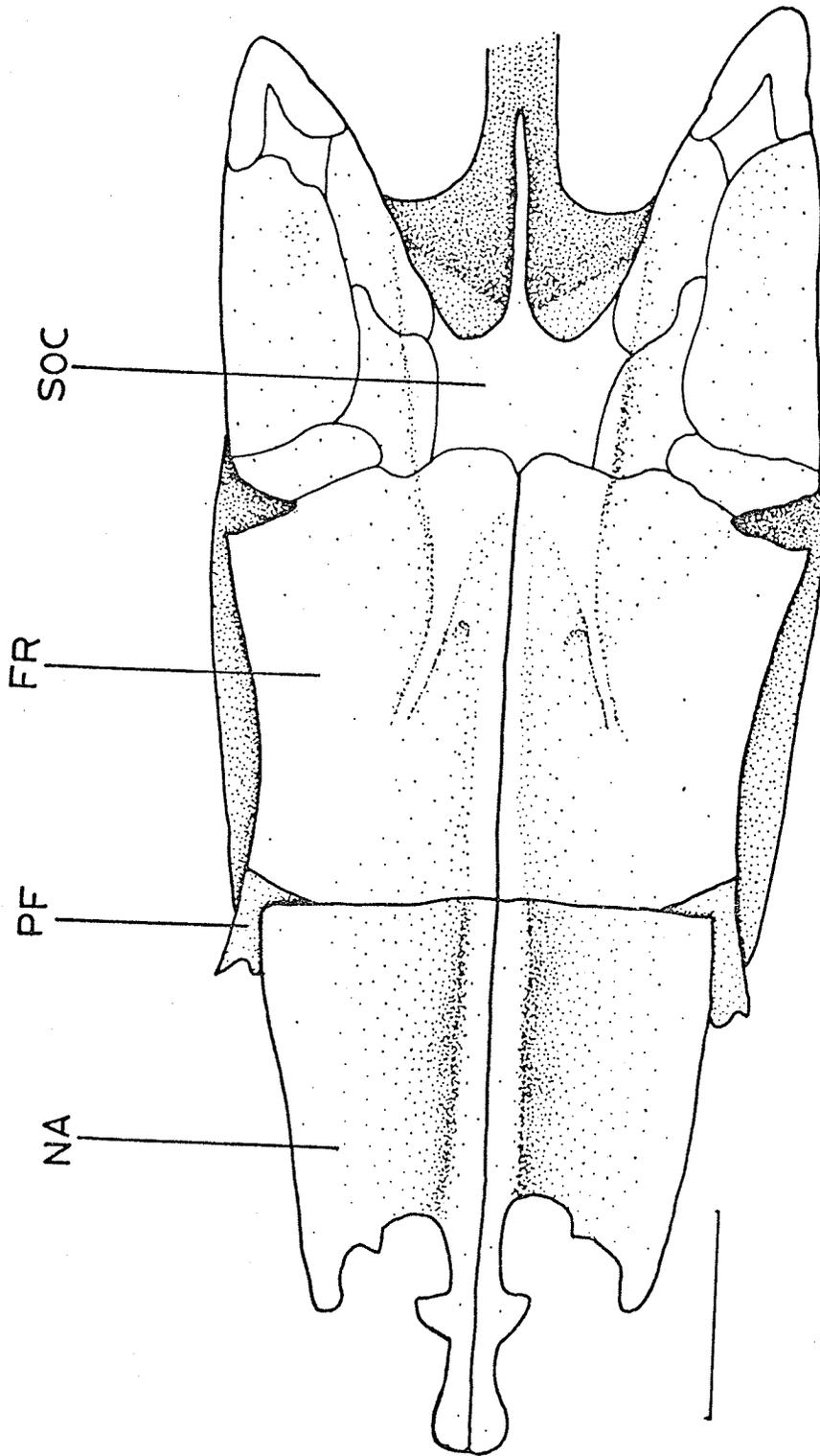


Figure 39. Lateral view of the skull of Abyssicola  
macrochir, USNM 77248, 75 mm HL.

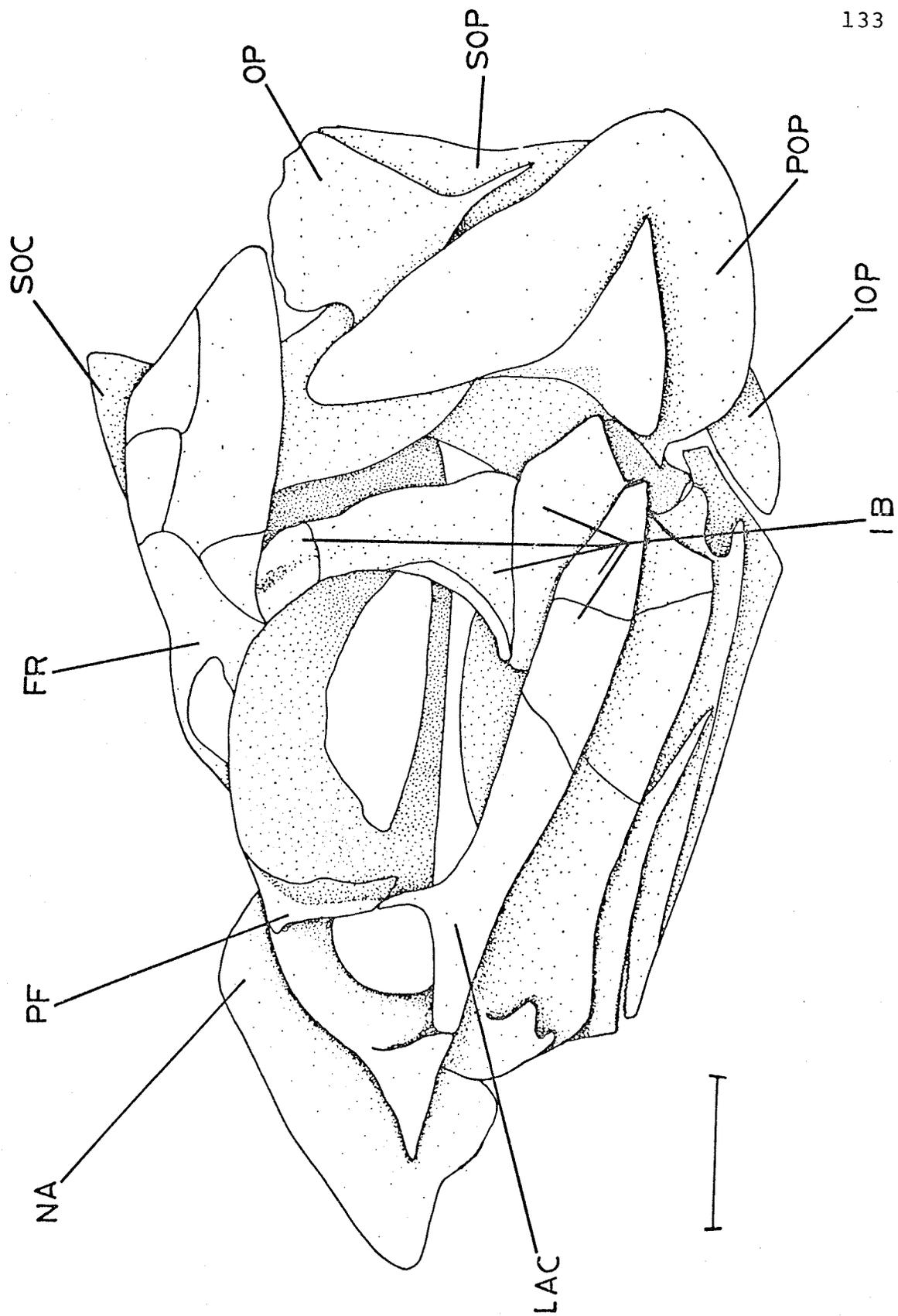


Figure 40. Dorsal view of the skull of Coelorinchus  
coelorinchus carminatus, MCZ 51169, 59 mm HL

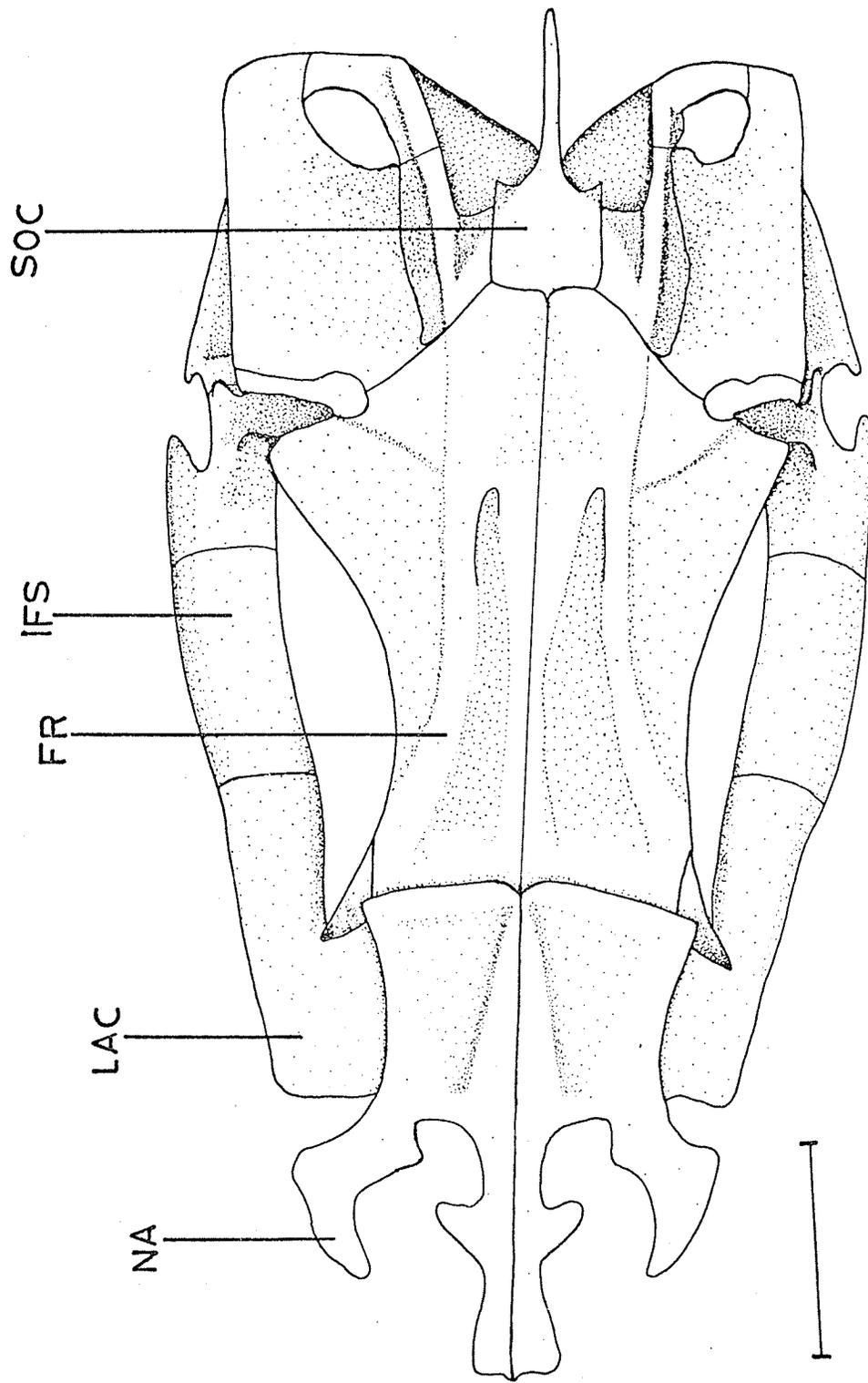


Figure 41. Lateral view of the skull of Coelorinchus  
coelorinchus carminatus, MCZ 51169, 59 mm HL.

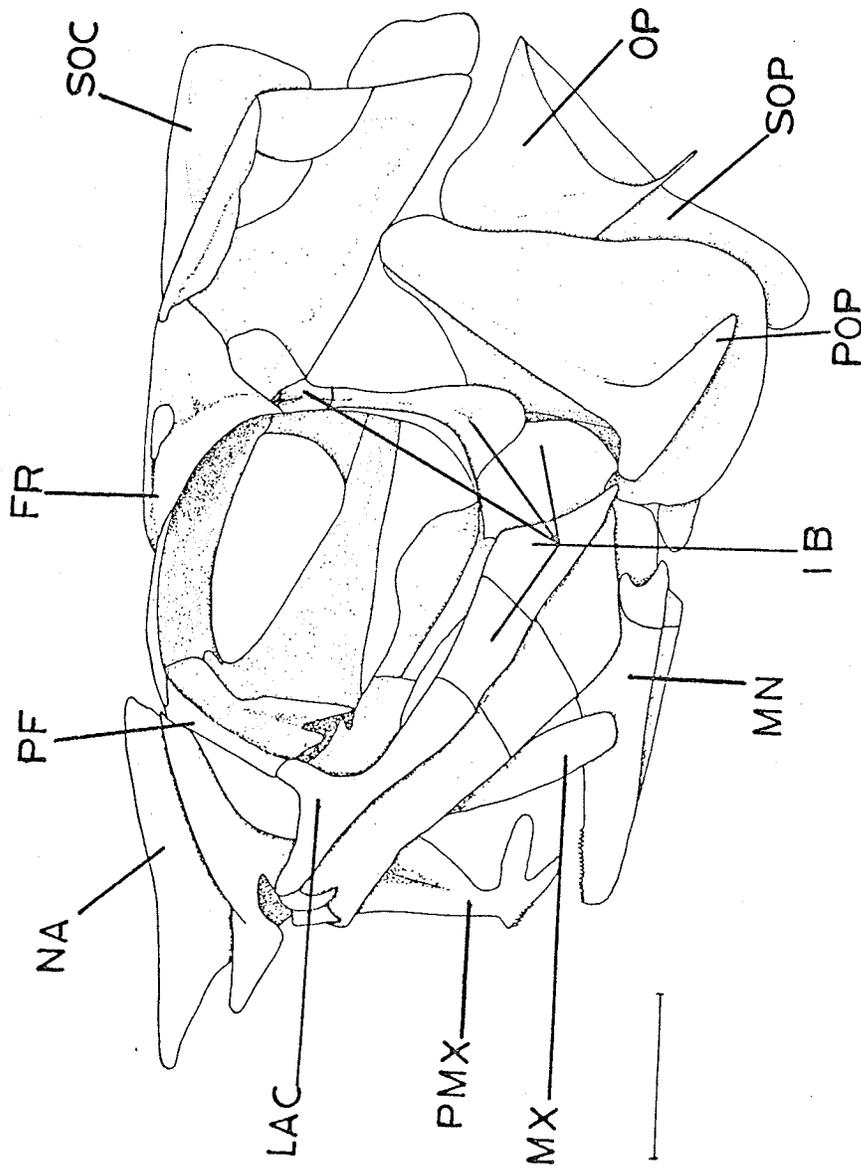


Figure 42. Dorsal view of the skull of Coelorinchus chilensis, LACM, Eltanin 1989, 51 mm HL.

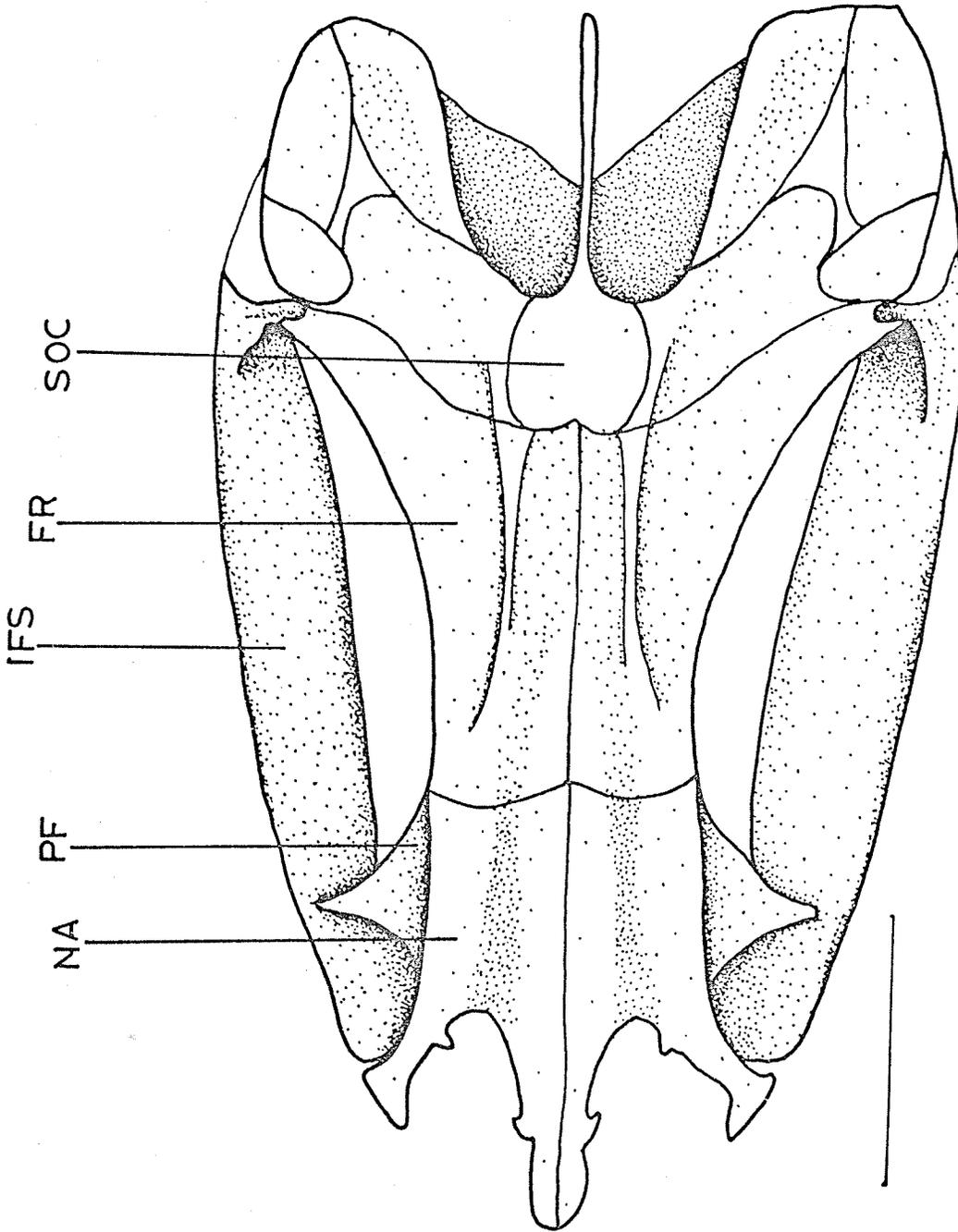


Figure 43. Lateral view of the skull of Coelorinchus chilensis, LACM Eltanin 1989, 51 mm HL.

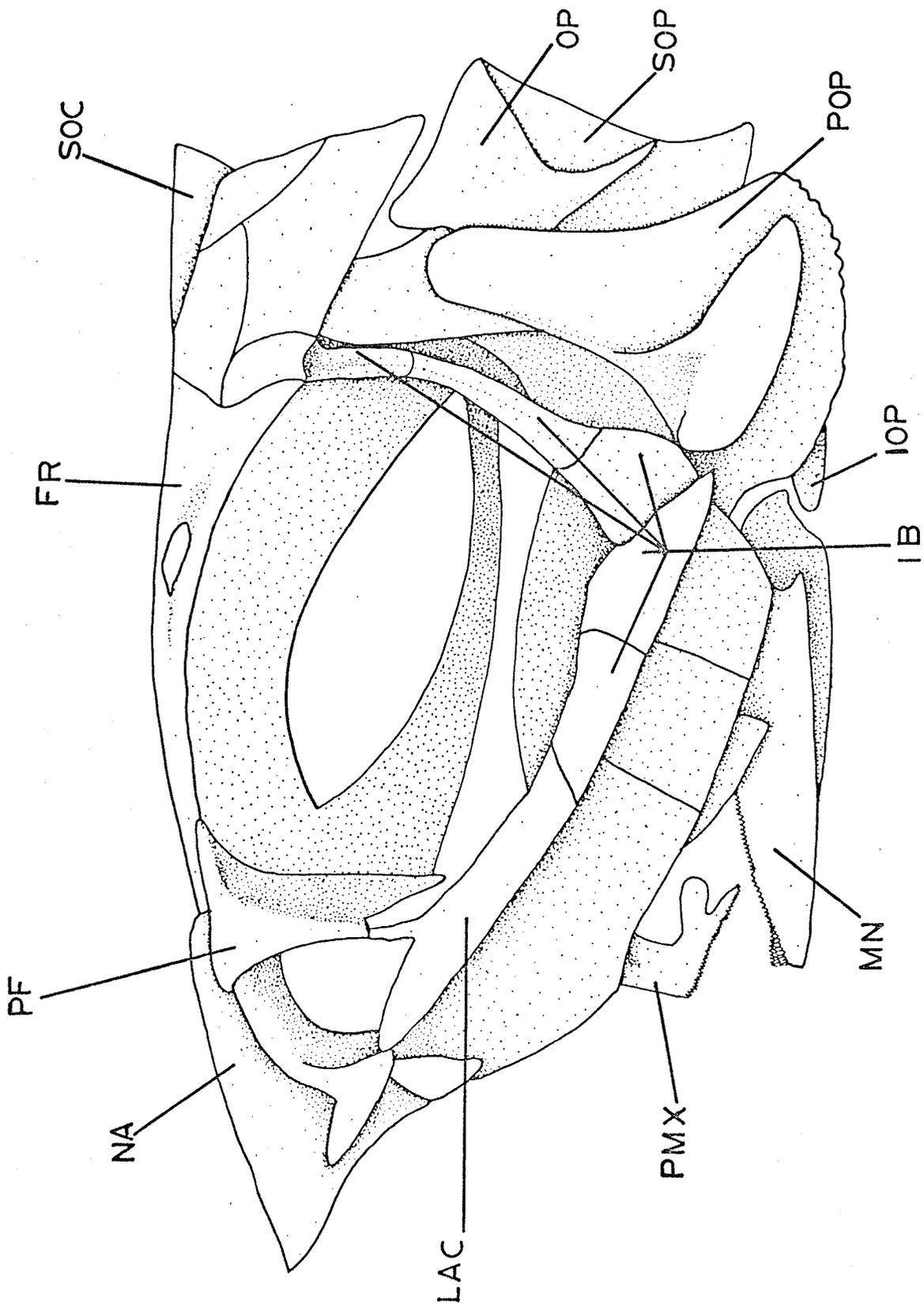


Figure 44. Dorsal view of the skull of Coelorinchus  
longissimus, MCZ 47740, 57 mm HL.

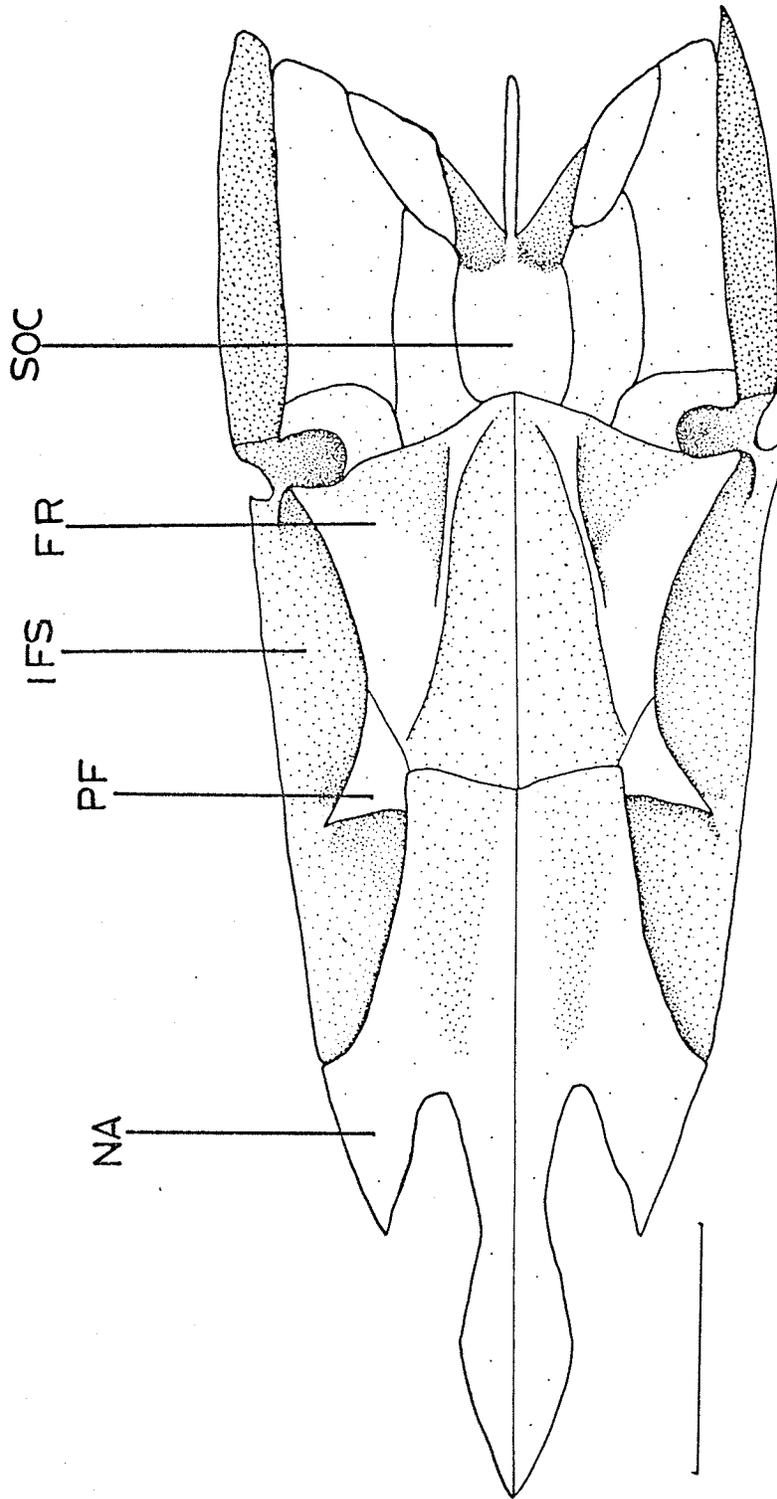
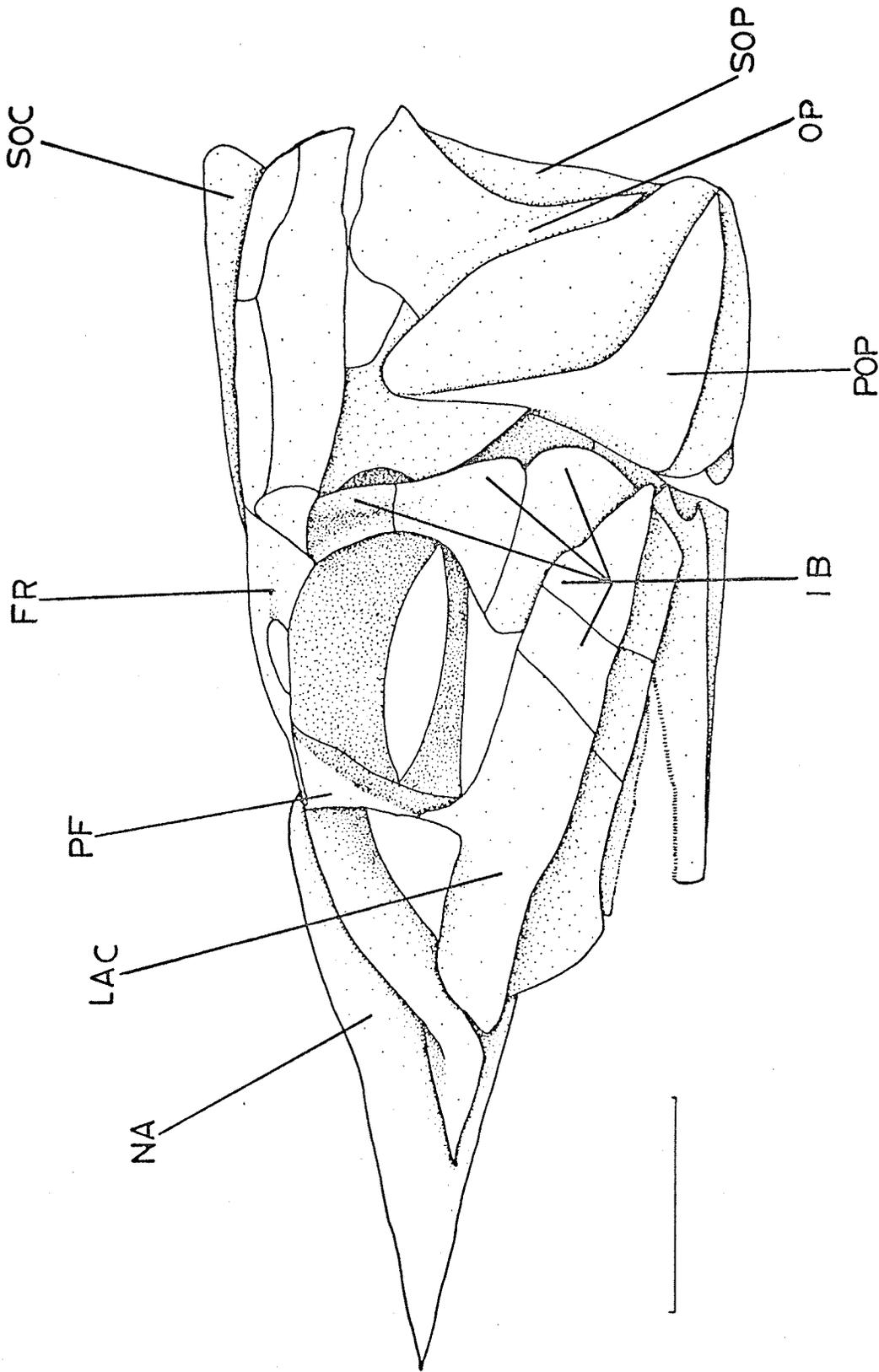


Figure 45. Lateral view of the skull of Coelorinchus  
longissimus, MCZ 47740, 57 mm HL.



The nasals of Coelorinchus occa are similar to those of the preceding species, with long, flat anterior processes. The distal end of the medial processes is round and the lateral processes are long and pointed anteriorly so that there is bone supporting most of the lateral margin of the rostrum (figures 46 and 47).

Coelorinchus jordani (figures 48 and 49), Coelorinchus innotabilis (figures 50 and 51) and Coelorinchus japonicus (figure 52) have nasals with entire lateral edges anterior to the nasal capsule. The lateral and medial processes prominent in the other species appear to have met distally, leaving a space where a lateral line passes that is in the same position as the notch between the two processes in other species. Coelorinchus jordani has short, broad nasals; those of Coelorinchus innotabilis are longer and narrower and Coelorinchus japonicus has long, wide nasals.

Trachyrincus helolepis has large nasals of thin bone that entirely fill the horizontal plane of the rostrum. They form a sharp point anteriorly and there is a small hole through them near the midline about halfway along the length (figures 53,54).

### III. Infraorbital Series

The lacrimal and five infraorbital bones form a series that extends from the ventral edge of the nasal capsule posteriorly ventral to the orbit, and then dorsally posterior to the orbit, to meet the cranium at the sphenotic. The lacrimal

Figure 46. Dorsal view of the skull of Coelorinchus  
occa, MCZ 51166, 117 mm HL.

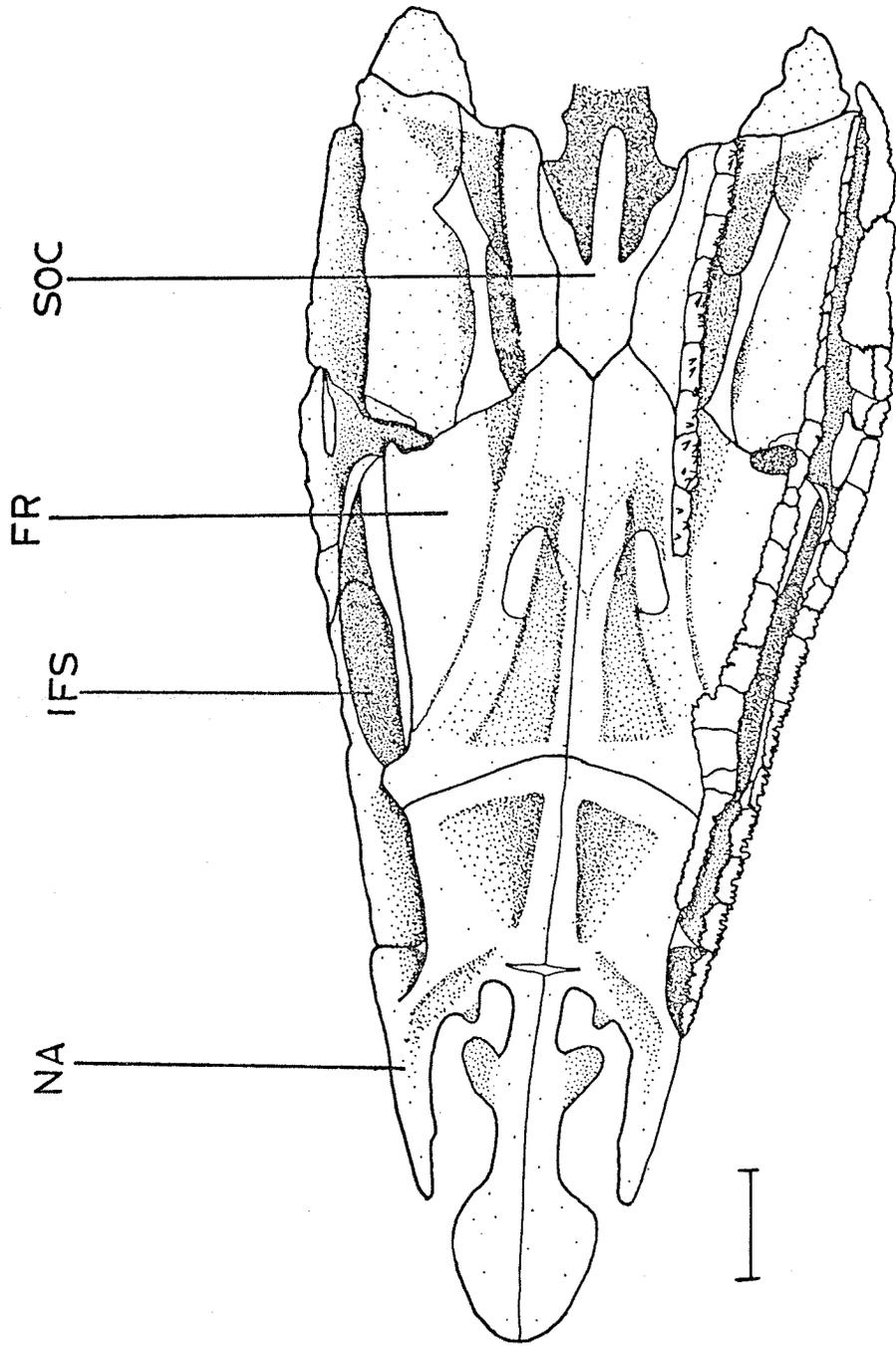


Figure 47. Lateral view of the skull of Coelorinchus  
occa, MCZ 51166, 117 mm HL.

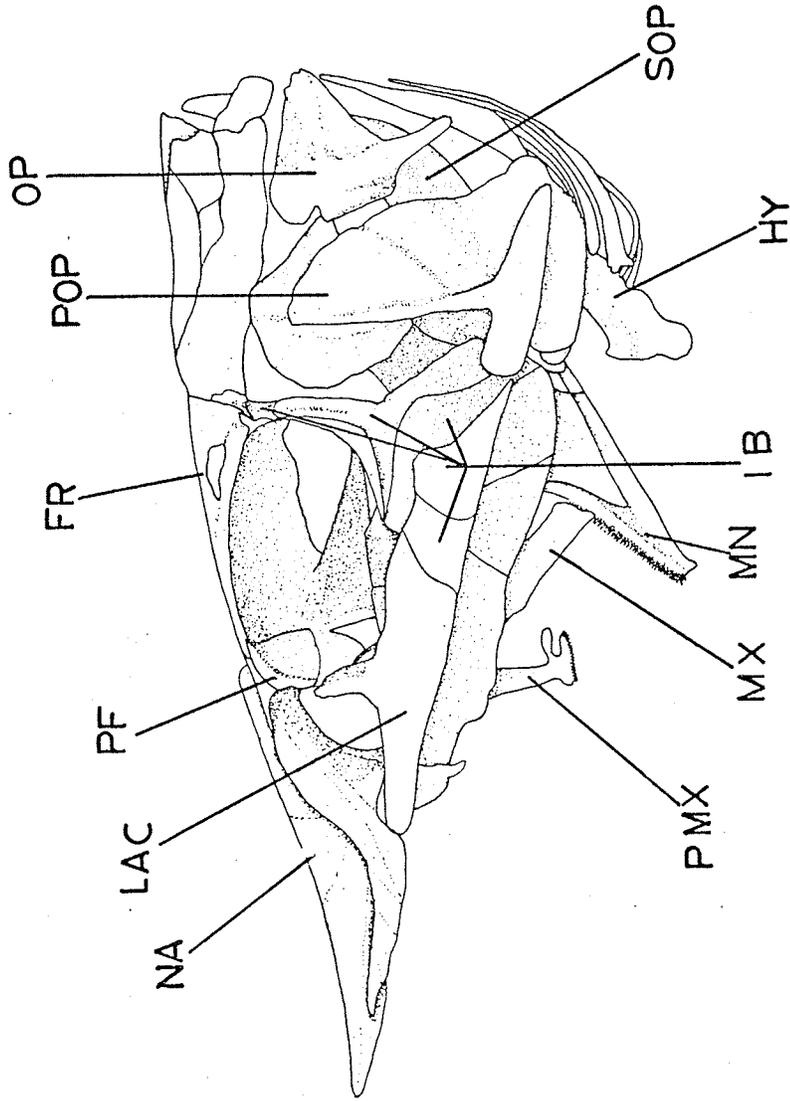


Figure 48. Dorsal view of the skull of Coelorinchus  
jordani, USNM 77197, 51 mm HL.

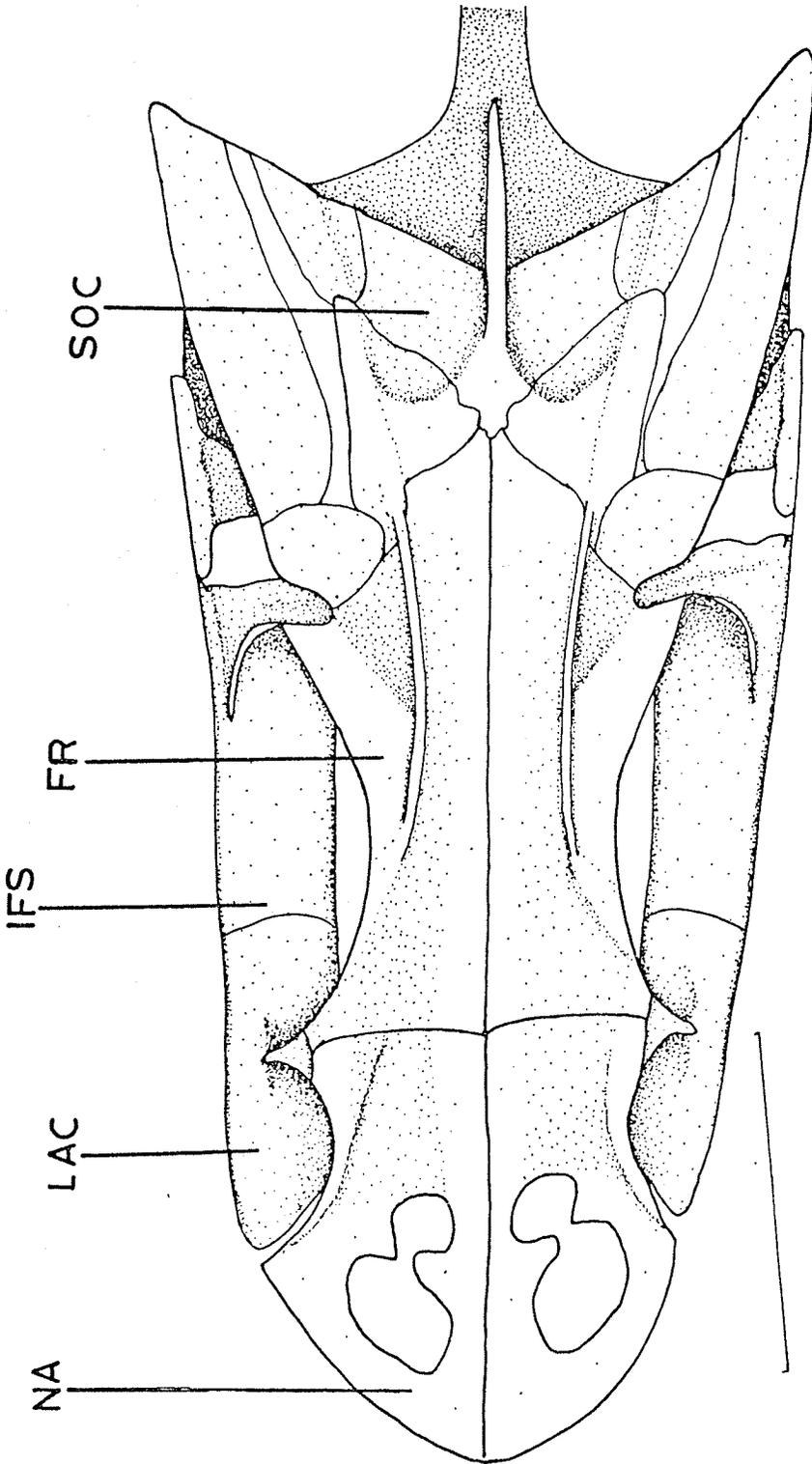


Figure 49. Lateral view of the skull of Coelorinchus  
jordani, USNM 77197, 51 mm HL.

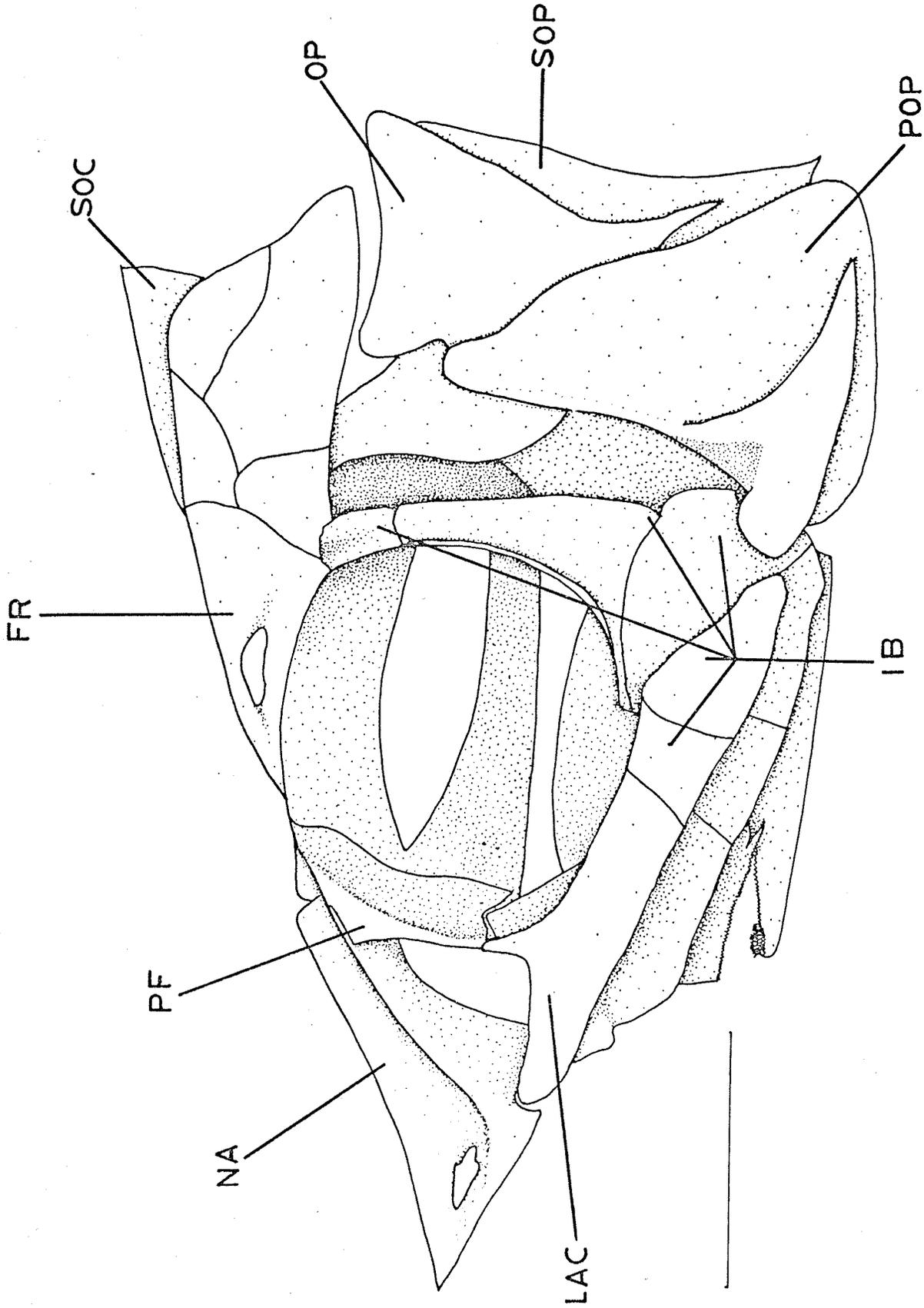


Figure 50. Dorsal view of the skull of Coelorinchus  
innotabilis, LACM Eltanin 1718, 54 mm HL.

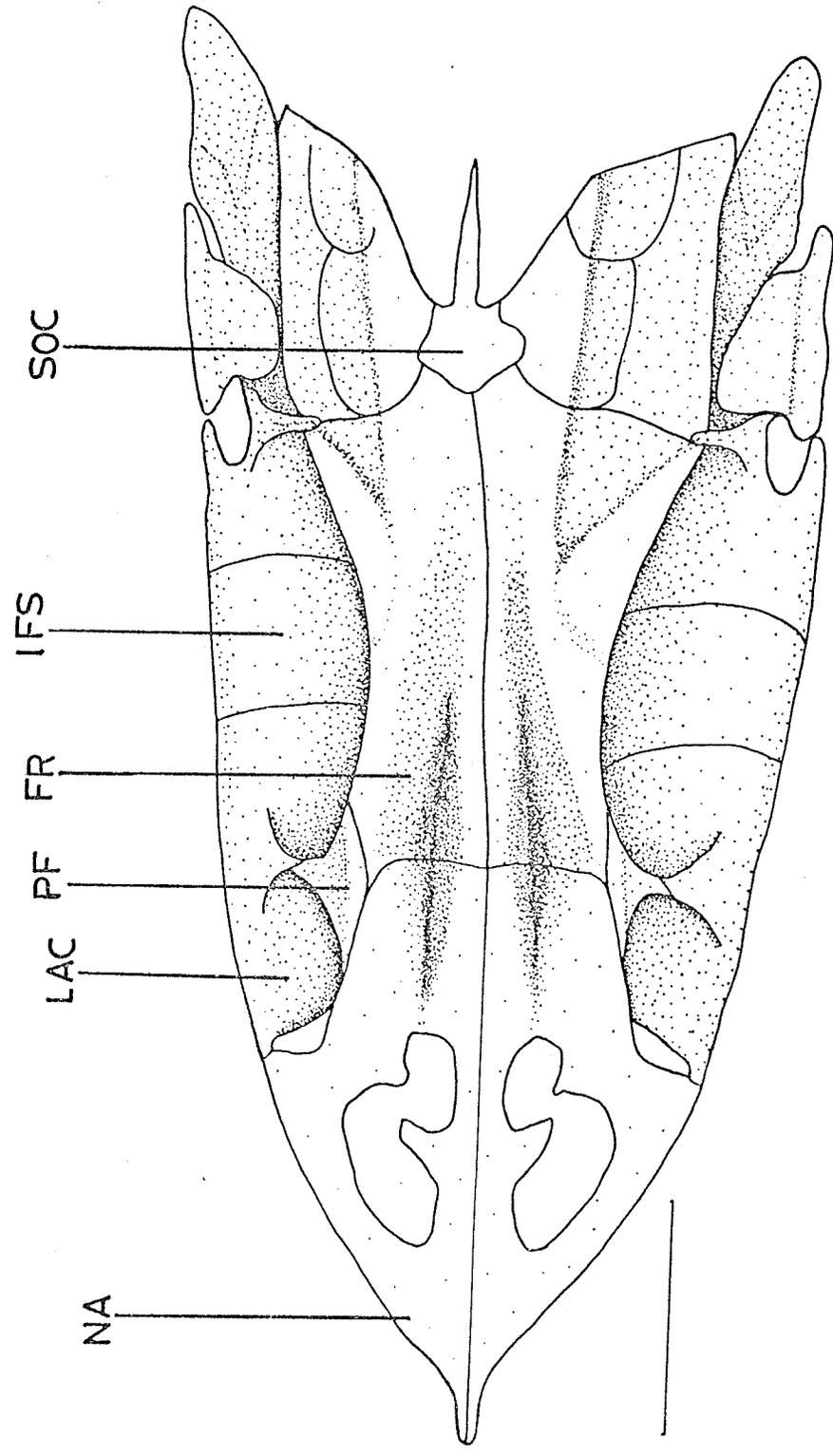


Figure 51. Lateral view of the skull of Coelorinchus  
innotabilis, LACM Eltanin 1718, 54 mm HL.

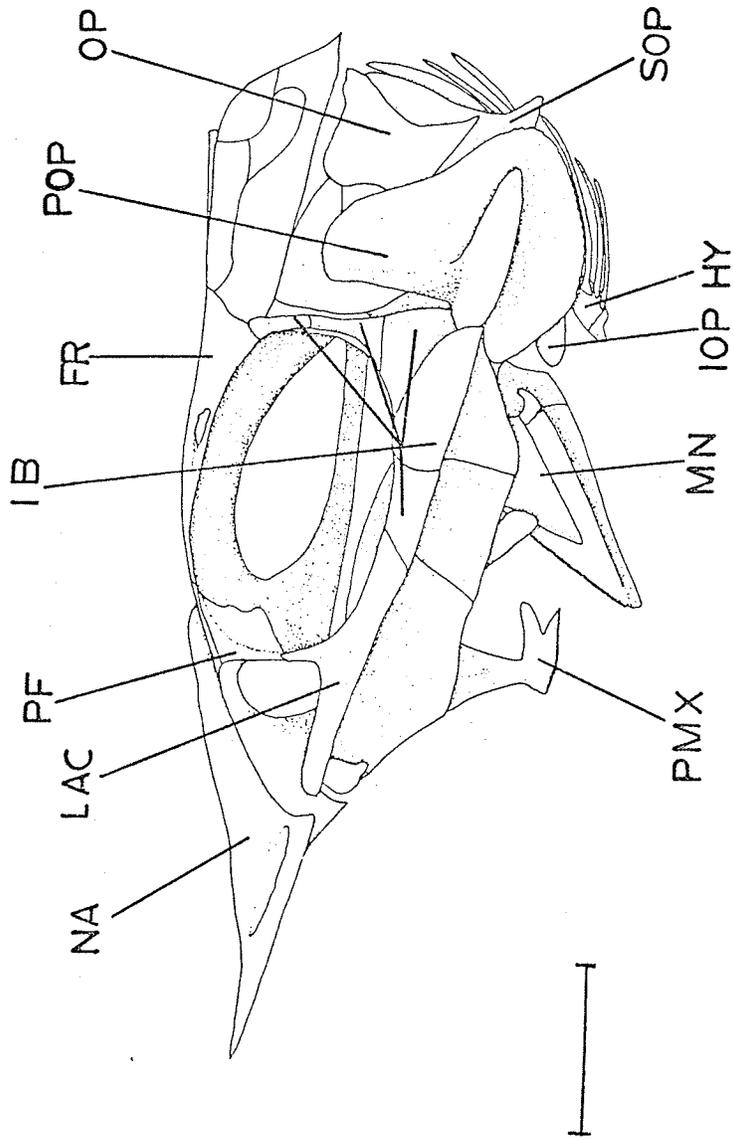
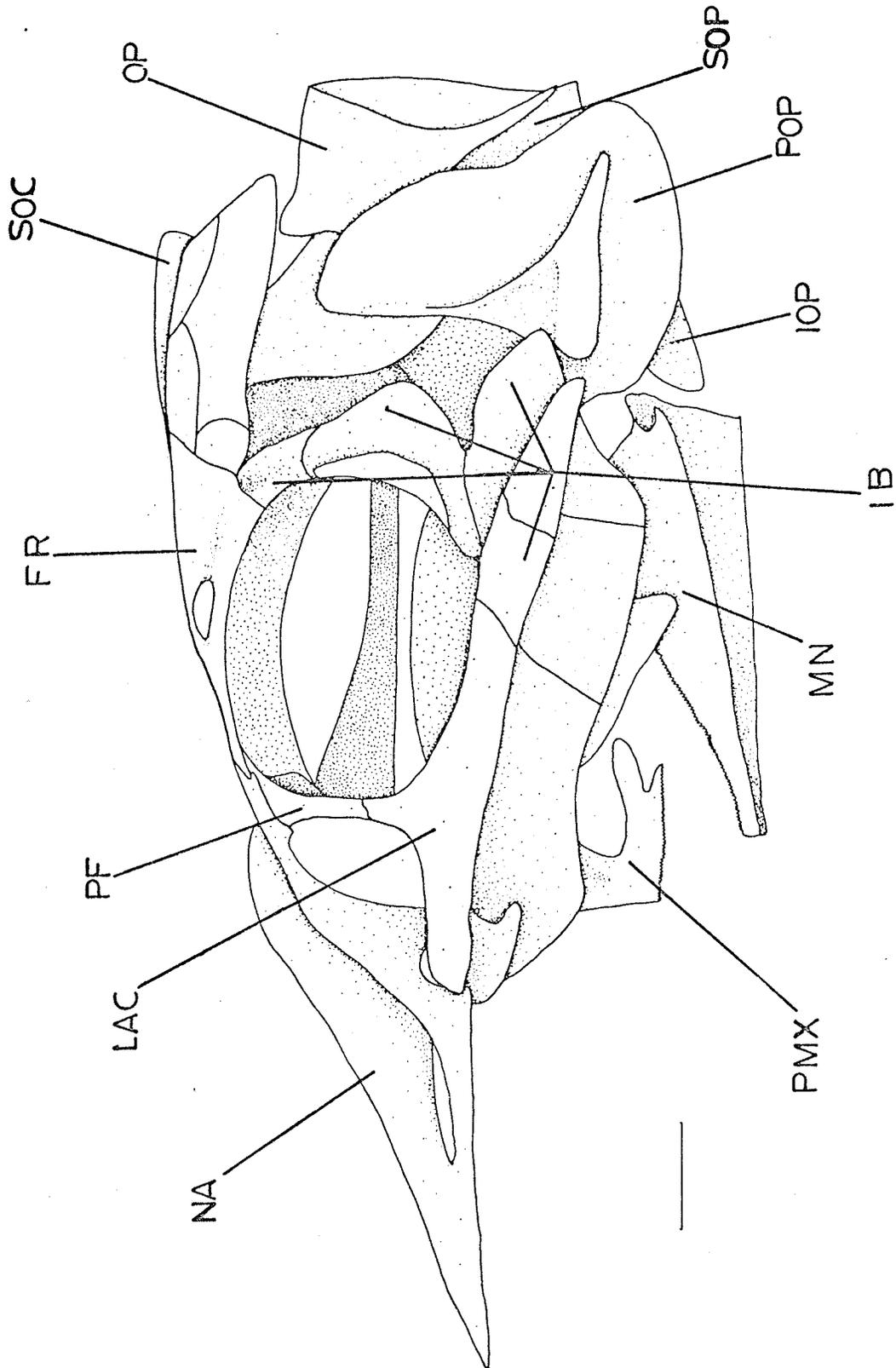


Figure 52. Lateral view of the skull of Coelorinchus japonicus, SU 7939, 121 mm HL.



spine is a process that extends from the dorsal surface of the lacrimal and meets the prefrontal dorsally; it is a distinct process in some species and absent in others.

The bones of the infraorbital series are very thin and have three surfaces, as if the bone had been folded at a dorso-medial and a dorsolateral angle, to form a wide medial surface, a broad horizontal surface and a lateral surface which forms the infraorbital ridge of the lacrimal and first two infraorbitals.

Macruronus novaezelandiae has a long, narrow lacrimal with a broad lacrimal spine (figure 14). The lateral surface of the lacrimal and first two infraorbitals is weak and there is no infraorbital ridge. The second infraorbital terminates posteriorly in a round corner; there is a small area of lateral surface on the third infraorbital just dorsal to the second. The fourth infraorbital is long and narrow and well ossified, appearing to be a flattened tube formed by the folding of the anterior and posterior edges laterally over the medial surface. The fifth infraorbital is small and concave.

Steindachneria argentea has a lacrimal with a small lateral surface developed only at the posterior and anterior ends of the bone, and continuous posteriorly with the lateral surface of the first three infraorbitals. There is no lacrimal spine and the widest part of the lacrimal is anterior to the orbit, ventral to the nasal capsule (figure 16).

The lacrimal of Bathygadus macrops is long and wide, bearing a distinct lacrimal spine that borders the ventral half of the anterior of the orbit (figure 18). The first three infraorbitals are small and set in a tight circle at the posteroventral corner of the orbit.

Lepidorhynchus denticulatus has a wide lacrimal with no distinct spine, though it curves dorsally around the anteroventral corner of the orbit to its most dorsal extension ventral to the prefrontal. The lateral surface extends anteriorly as far as the medial surface does, and with the lateral surface of the first two infraorbitals forms a small infraorbital ridge. The second infraorbital terminates posteriorly in a narrow point (figure 19).

Malacocephalus occidentalis has a small lacrimal spine and the lateral surface of the lacrimal extends anteriorly to the ventral side of the lateral process of the nasal (figure 21). The lateral surface of the second infraorbital is triangular and there is a weak infraorbital ridge.

The infraorbital series of Nezumia bairdii is similar to that of M. occidentalis, except that the lacrimal curves dorsally around the anteroventral corner of the orbit and there is no distinct lacrimal spine (figure 23).

Mataeocephalus acipenserinus has a broad lacrimal with no spine (figure 25). The lateral surface of the lacrimal extends anteriorly as far as the medial surface, and the

horizontal surface forms a broad shelf ventral to the nasal capsule. The infraorbital shelf is very broad, and the lateral surface of the lacrimal and first two infraorbitals forms a strong ridge ventral to the orbit (figure 24). The second infraorbital terminates posteriorly in a blunt corner.

Coryphaenoides rupestris has wide lacrimal and infraorbital bones, with a broad shelf ventral to the orbit (figure 27). There is no lacrimal spine and the lateral surface of the lacrimal terminates anteriorly directly ventral to the prefrontal. The second infraorbital has a triangular lateral surface.

There is a broad lacrimal spine in Coryphaenoides carapinus (figure 29). The lacrimal and first two infraorbitals form a broad shelf and a pronounced infraorbital ridge. The lateral surface of the second infraorbital is round posteriorly.

Coryphaenoides armatus has a sharp lacrimal spine and a narrow infraorbital shelf (figure 31). The orbit is small and the posteroventral corner of the orbit is sharp so that the dorsal edge of the second infraorbital does not border the orbit.

Coryphaenoides acrolepis has a large orbit and a pronounced lacrimal spine (figure 33). The lateral surface of the lacrimal extends anteriorly as far as the ventral edge of the nasal capsule. The infraorbital shelf is narrow and slants ventroposteriorly, so that it does not border the orbit posteriorly.

Coryphaenoides leptolepis has a small orbit, sharp lacrimal spine and narrow infraorbital shelf (figure 35). It differs from the other species of Coryphaeoinoides mentioned here in that the lateral surface of the lacrimal is continuous anteriorly with a small flap of bone, present in the other species, which encases a lateral line canal. The second infraorbital terminates posteriorly in a sharp corner.

Coryphaenoides pectoralis has a short lacrimal spine anterior to the prefrontal which does not border the anterior edge of the orbit. The lateral surface of the lacrimal and first two infraorbitals is small and the infraorbital shelf is narrow (figure 36).

The orbit of Macrourus berglax is very large and there is a stout lacrimal spine and moderately wide infraorbital shelf (figures 2 and 4). The lateral surface of the lacrimal extends anteriorly as far as the posterior edge of the lateral process of the nasal and the posterior edge of the lateral surface of the second infraorbital is a sharp corner.

The infraorbital series of Abyssicola macrochir and the seven species of Coelorinchus examined share a number of characteristics. There is a pronounced lacrimal spine bordering the ventral third of the anterior edge of the rectangular orbit. The lateral surface of the lacrimal extends anteriorly to the posteroventral corner of the lateral process of the nasal, where the horizontal surface of the lacrimal forms a

broad shelf ventral to the nostril (figures 39 through 53). The lacrimal and first two infraorbitals form a broad shelf ventral to the orbit and a strong infraorbital ridge, terminating posteriorly in a sharp corner close to the "shelf" of the preopercle.

The infraorbital series of Trachyrincus helolepis consists of narrow bones that form a broad subocular shelf, as described by Regan (1903) (figures 54 and 55). The third infraorbital has a long posterior process dorsally which extends over the preopercle dorsal to the preopercular shelf.

#### IV. Suspensorium and Preopercle

The bones of the suspensorium have been described on page 35. There is some variation in the overall shape of this mechanical unit within the group, and a great deal of variation in the shape and size of the preopercle.

The suspensorium in those species with deep, laterally compressed heads (for example, Bathygadus macrops, Malacocephalus occidentalis and Coryphaenoides pectoralis) is deep dorsoventrally, while that of those with depressed heads is elongate anteroposteriorly and shorter (Okamura, 1970b).

The preopercle is a thin bone attached anteriorly to the posterior edge of the hyomandibula, symplectic and quadrate. The anterior edge of the preopercle curves anteriorly along the ventral portion of the bone. The two divisions of the adductor mandibulae muscle,  $A1\alpha$  and  $A1\beta$ , which insert on

Figure 53. Dorsal view of the skull of Trachyrincus  
helolepis, SOSC Reg. No. 309, 98 mm HL.

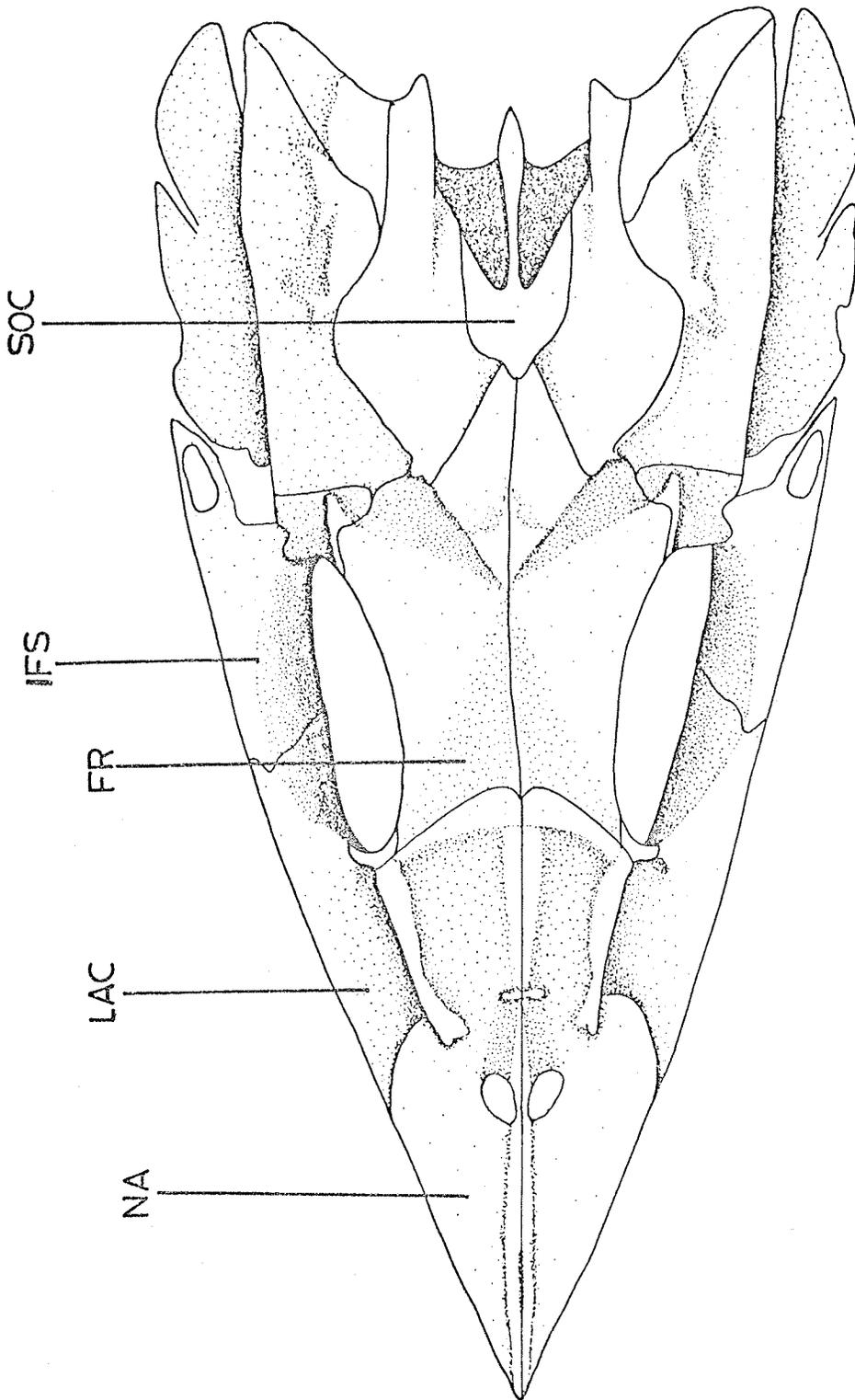


Figure 54. Lateral view of the skull of Trachyrincus  
helolepis, SOSC Reg. No. 309, 98 mm HL.

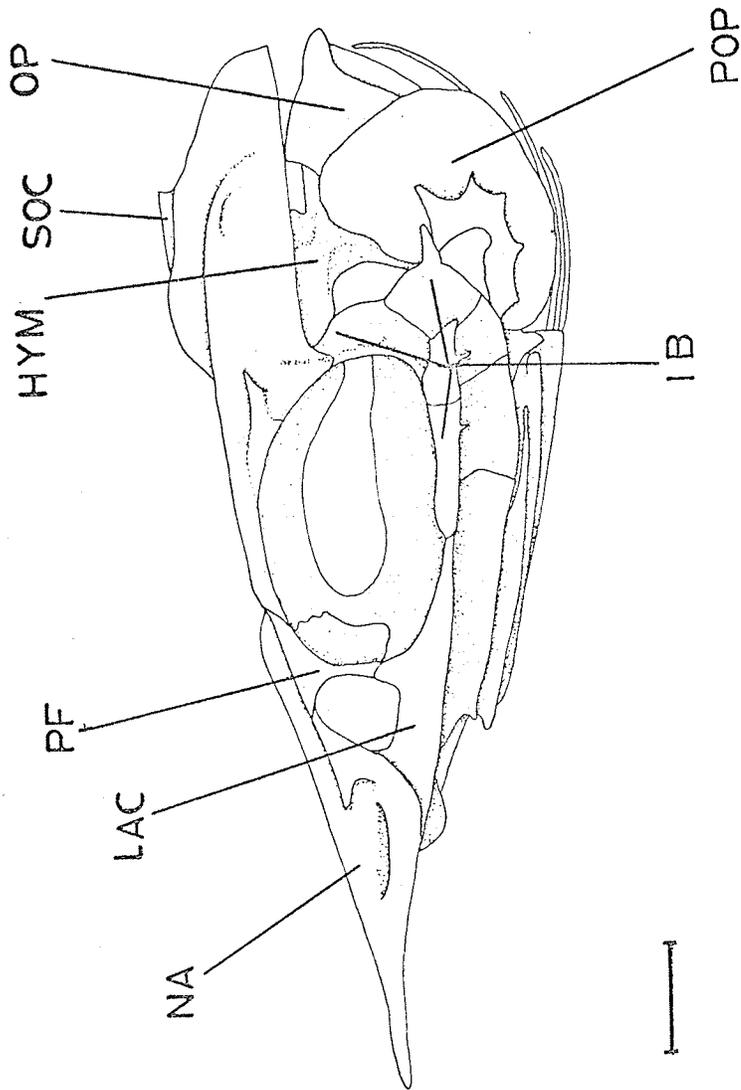
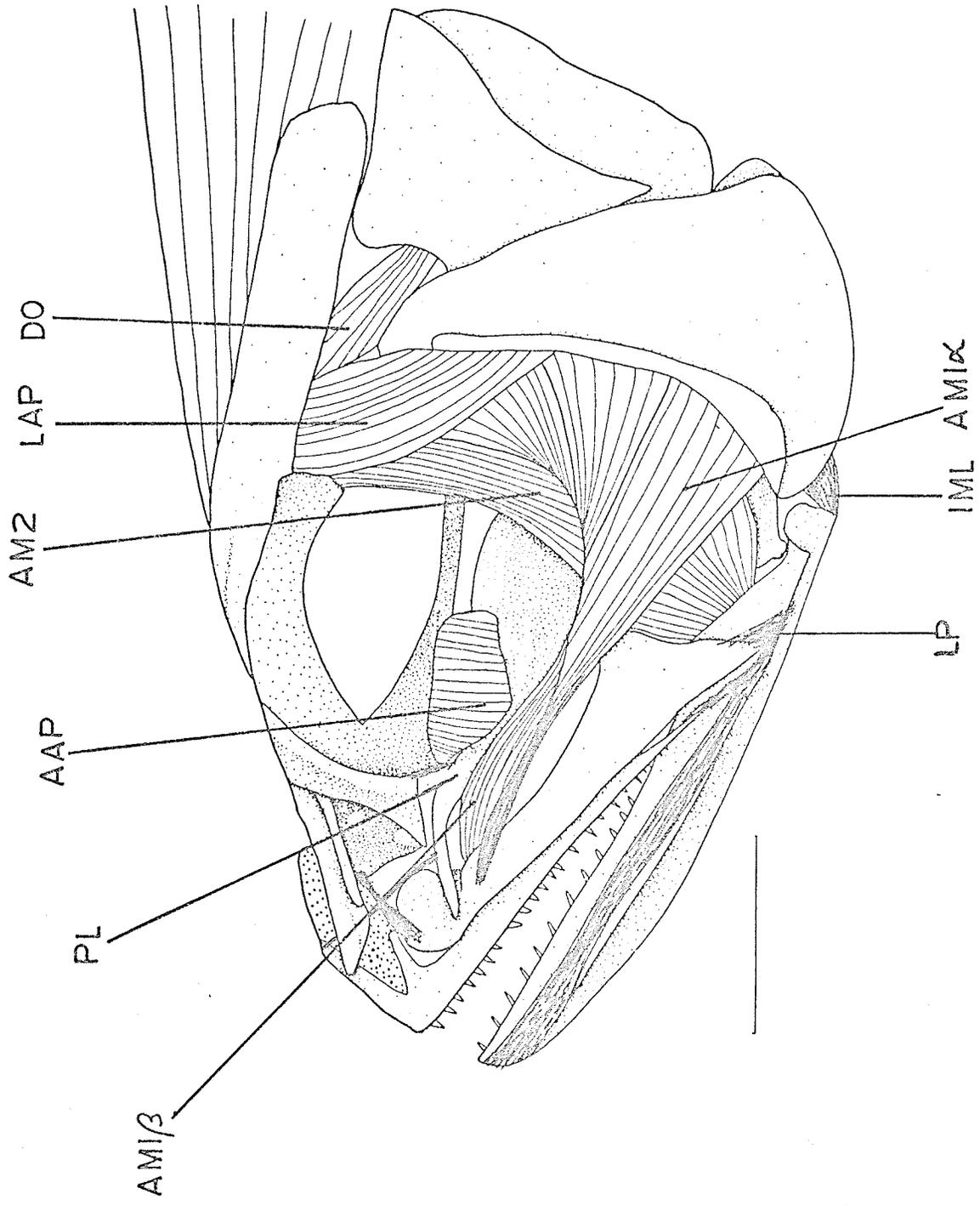


Figure 55. Lateral view of the superficial cheek muscles of Macruronus novaezelandiae, MCZ 48944, 59 mm HL.



the maxilla originate on the preopercle and the other suspensorial bones immediately anterior to it. At the ventral edge of the muscles, the anterior edge of the preopercle curves dorsally, so that it runs along the muscle anteriorly in many species. The anterior edge of the preopercle is "folded" back over the main portion of the bone to form a process which will be called the preopercular shelf. In many macrourids the preopercular shelf is large and forms a posterior extension of the infraorbital ridge.

The least specialized condition of the preopercle is found in Macruronus novaezelandiae, where it is a slender crescent that slopes anteroventrally (figure 14). The preopercular shelf is long and narrow, extending for most of the length of the anterior edge of the preopercle.

Steindachneria argentea has a posteriorly rounded preopercle with a straight anterior edge (figure 16). The small preopercular shelf consists of two small triangles, which were found to vary among the few specimens examined in their size and position.

The preopercle of Bathygadus macrops is not very different from that of M. novaezelandiae, being crescent shaped and slanted anteroventrally (figure 18). The shelf is round and its largest area is ventral to the muscle insertion.

The anterior edge of the preopercle of Lepidorhynchus denticulatus is long and straight (figure 19). The preoperc-

ular shelf is small and its posteroventral corner is square. The anterior edge forms a right-angled notch at the ventral side of the insertion of adductor mandibulae muscles. Ventral to the shelf the preopercle is expanded posteriorly and anteriorly, covering the interopercle laterally.

The preopercle of Malacocephalus occidentalis is similar to that of the preceding species, except that the shelf is larger and expanded ventrally (figure 21).

Nezumia bairdii has a preopercle that is wider dorsally than those of L. denticulatus and M. occidentalis. The shelf is wide and round with most of its area ventral to the notch in the anterior edge (figure 23).

The preopercle of Mataeocephalus acipenserinus is broad dorsally and the shelf is entirely ventral to the site of muscle attachment (figure 25). The shelf is narrow dorsally and the ventral edge is wide and round.

Coryphaenoides rupestris has a preopercle that is narrow dorsally and wide ventrally (figure 27). The preopercular shelf is moderate in size, with several partially ossified processes that form struts around the lateral line canal which is posterior and ventral to the shelf in all species.

The preopercle of Coryphaenoides carapinus is shaped like a broad triangle with round corners (figure 29). The shelf is narrow, round and directed posteriorly. The anterior edge does not form a sharp notch, but curves slightly antero-

dorsally.

In Coryphaenoides armatus (figure 31), Coryphaenoides acrolepis (figure 33), Coryphaenoides leptolepis (figure 35) and Coryphaenoides pectoralis (figure 36) the preopercular shelf is small, with a straight ventral edge and rounded anterior and posterior edges. The curve at the ventral side of the muscle attachment is nearly a right angle. The shelf of C. leptolepis is longer anteroposteriorly than in the other species.

The preopercle of Macrourus berglax is wide dorsally, and the anterior and posterior edges of the dorsal portion are straight (figure 2). The shelf is triangular and the posterior corner is a sharp point directed posteriorly. The anterior edge curves to be nearly horizontal ventral to the insertion of the adductor mandibulae 1  $\alpha$ .

Abyssicola macrochir has a shallow preopercular shelf with a very sharp corner posteriorly (figure 39). The preopercle widens gradually ventrally and the ventral edge is round. The anterior edge curves to an angle of about 45 degrees.

In all species of Coelorinchus examined, as in M. berglax and A. macrochir, the preopercular shelf forms a posterior continuation of the infraorbital ridge, though the second infraorbital does not come in contact with the preopercular shelf and motion between these two parts of the ridge is

possible. There are large scales attached directly to the preopercular shelf, similar to those on the lacrimal and first two infraorbitals.

Coelorinchus coelorinchus carminatus has a preopercle with a narrow dorsal portion widening ventrally to a round ventral edge (figure 41). The shelf is long and narrow, terminating posteriorly in a sharp point.

In Coelorinchus chilensis the dorsal portion of the preopercle is narrower than in C. c. carminatus, and the ventral portion is wider (figure 43). The preopercular shelf extends posteriorly as far as the posterior edge of the medial part of the preopercle.

The dorsal portion of the preopercle in Coelorinchus longissimus is very wide and the ventral edge is straight (figure 45). The shelf extends posteriorly to the posterior edge of the preopercle and the anterior edge curves antero-dorsally.

Coelorinchus occa has a preopercle with a round dorsal portion and a small ventral portion (figure 47). The shelf is wide and long, and extends posteriorly almost to the posterior edge of the preopercle and anteriorly over the medial surface of the third infraorbital. The anterior edge of the preopercle makes a right angle ventral to the origin of the adductor mandibulae.

The preopercle of Coelorinchus jordani has a narrow dorsal portion widening ventrally both anteriorly and post-

eriorly (figure 49). The ventral edge is straight. The shelf extends anteriorly over the third infraorbital, as in Coelorinchus occa, and is sharply pointed posteriorly.

The preopercles of Coelorinchus innotabilis (figure 51) and Coelorinchus japonicus (figure 52) are short and wide dorsally and are deep and round ventrally. The narrow shelf extends anteriorly over the medial surface of the third infraorbital and posteriorly about three quarters of the way to the posterior edge of the preopercle. There is a right-angled notch in the anterior edge just ventral to the muscle attachment.

Trachyrinchus helolepis has a preopercle that is round on the dorsal, posterior and ventral edges and deeply notched anteriorly (figure 54). The preopercular shelf emanates from the deep anterior notch and is of the same width for its entire length. As in Coryphaenoides rupestris there are several partially ossified processes extending from the posterior and ventral edges of the shelf that form struts over the lateral line canal.

#### v. Opercular Series.

There is little variation in the opercular series among the species examined. The interopercle is wide, thin and oval in most macourids, but is smaller, rectangular and of thicker bone in Macrourus berglax, Abyssicola macrochir and Coelorinchus species. In Trachyrinchus helolepis the opercle and subopercle are very small and the interopercle is very long

and narrow.

#### VI. Jaws: Premaxilla, Maxilla and Mandible

The greatest variation in the jaws is in the lengths of the ascending and alveolar processes of the premaxilla. There are differences between species in the width of the head of the maxilla and the distance between the points of insertion of the primordial ligament and adductor mandibulae 1  $\beta$  on the maxilla. The mandible differs between species in length and in the development of a posterior socket at the articulation of the quadrate

In Macruronus novaezelandiae (figure 55), Steindachneria argentea (figure 56) and Bathygadus macrops (figure 57) the ascending processes of the premaxilla are short and the alveolar processes are long. The rostral cartilage is large and enters into the dorsal profile of the head when the mouth is closed, giving the snout a square appearance. The post-maxillary processes of these species are small. The teeth are large and separated from each other in Macruronus novaezelandiae and Steindachneria argentea, and are very small, numerous and in wide bands in Bathygadus macrops.

The maxilla in Macruronus novaezelandiae, Steindachneria argentea and Bathygadus macrops is narrow anteriorly and has small condyles and no distinct process at the insertion of the primordial ligament. The mandible of these species is long, and there is a shallow socket for the quadrate in Macruronus novaezelandiae.

Figure 56. Lateral view of the superficial cheek muscles of Steindachneria argentea, USNM 188852, 42 mm HL.

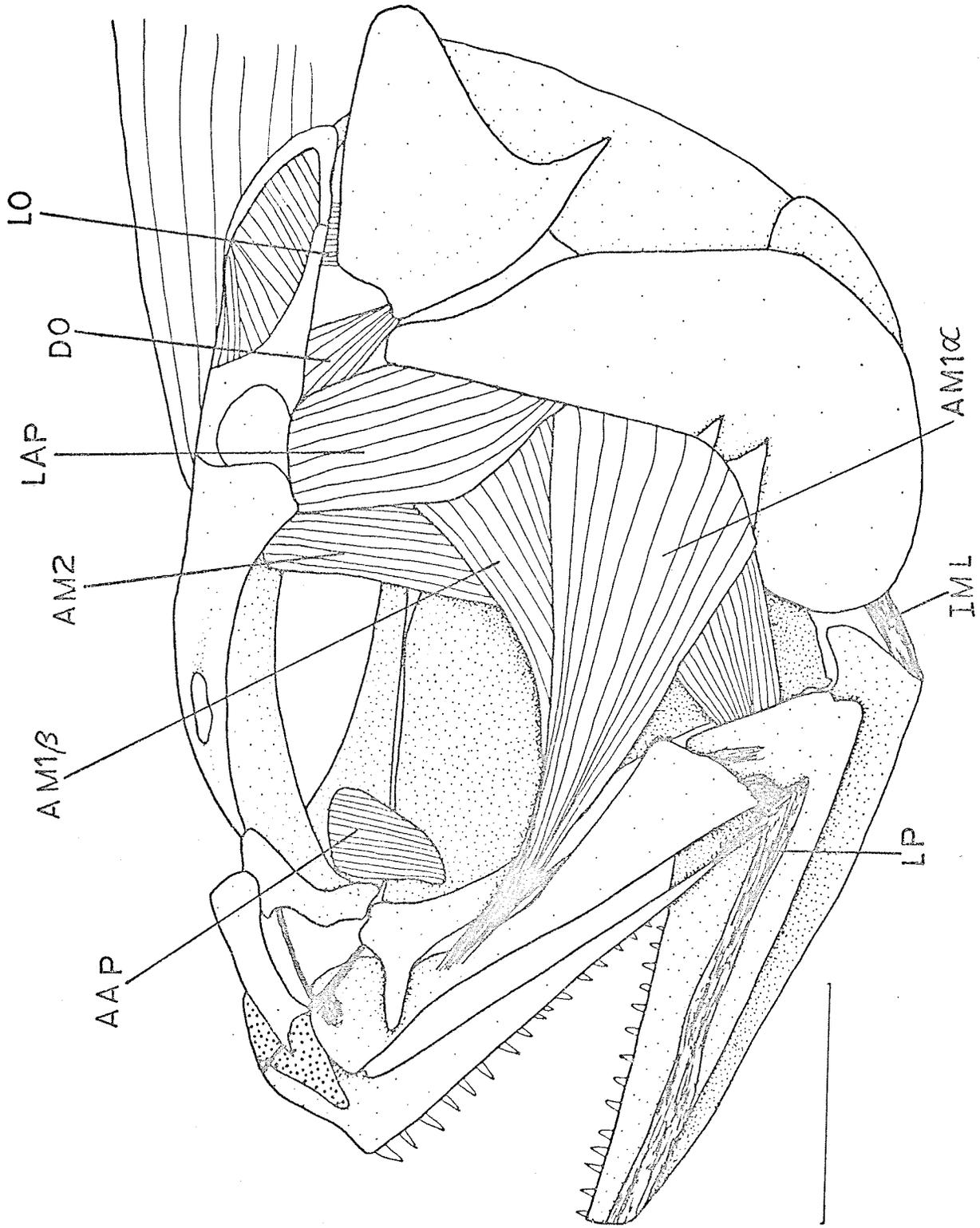
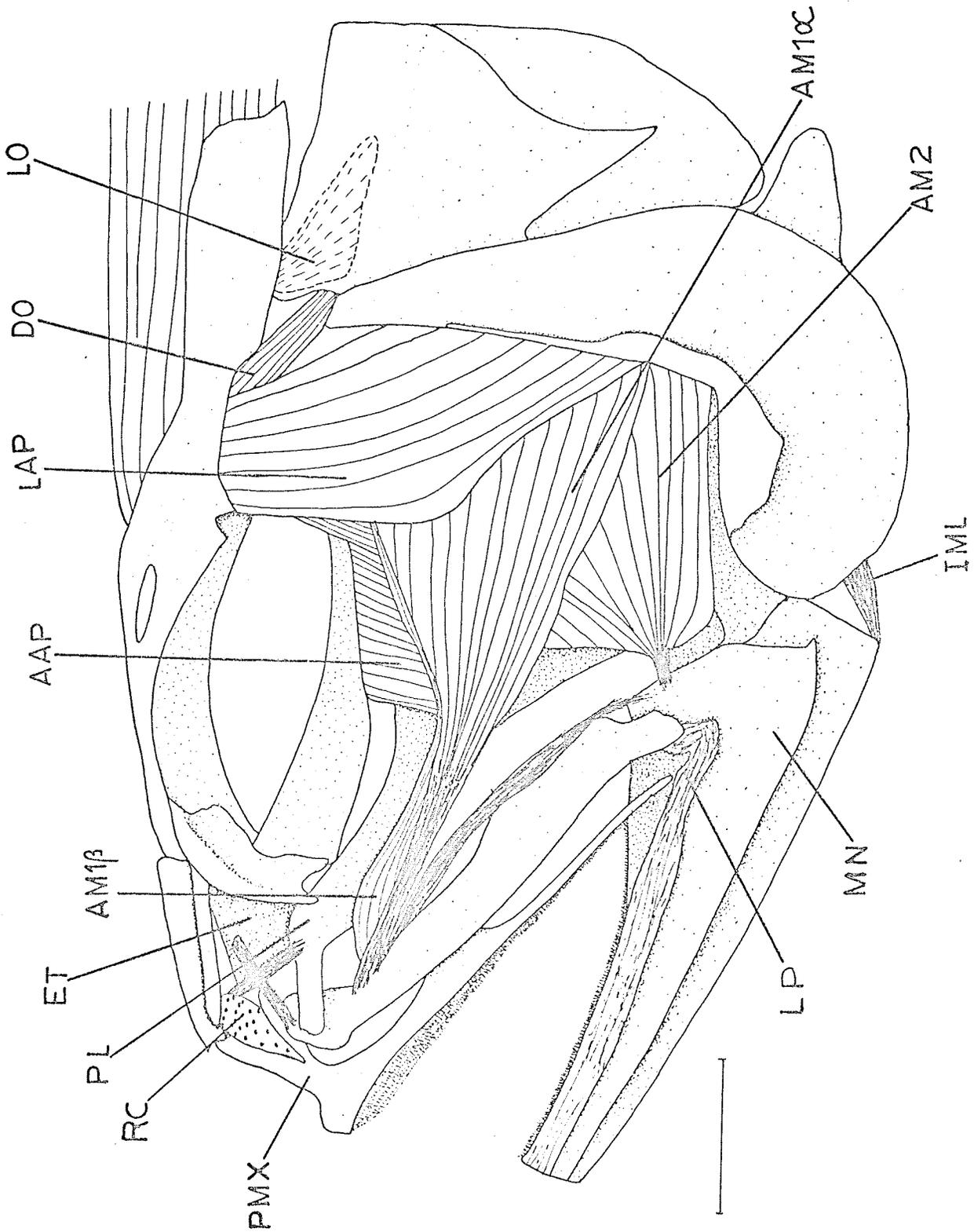


Figure 57. Lateral view of the superficial cheek  
muscles of Bathygadus macrops, UMML 15193, 68 mm HL.



The ascending processes of the premaxilla of Lepido-  
rhynchus denticulatus are moderately long and the long alveolar  
process bears few large teeth (figure 58). The maxilla has  
a large head with a small premaxillary condyle and a shallow  
process at the insertion of the primordial ligament.

Malacocephalus occidentalis has moderately long ascending  
processes of the premaxilla and the alveolar process is long  
with moderately long teeth (figure 59). There is a thin  
postmaxillary process of the premaxilla which is distinct  
from the dorsal edge of the alveolar process. The maxilla  
has a well-differentiated head with a deep groove for the  
maxillary process of the palatine. The premaxillary condyle  
is moderately large and the posterior ramus of the maxilla  
is long and moderate in width.

The premaxilla of Nezumia bairdii has a moderately long  
ascending process and a moderate alveolar process bearing  
a small postmaxillary process (figure 60). The maxilla has  
a large, square premaxillary condyle, a deep groove for the  
articulation of the palatine and a shallow process at the  
insertion of the primordial ligament.

The ascending processes of the premaxillae of Mataeo-  
cephalus acipenserinus are long and the alveolar processes  
are short (figures 61 and 97B). In ventral view the alveolar  
processes border only the anterior edge of the mouth and do  
not curve posteriorly to border the lateral edges (figure 87).

The postmaxillary process is long and wide, extending

Figure 58. Lateral view of the superficial cheek muscles of Lepidorhynchus denticulatus, MCZ 51515, 57 mm HL.

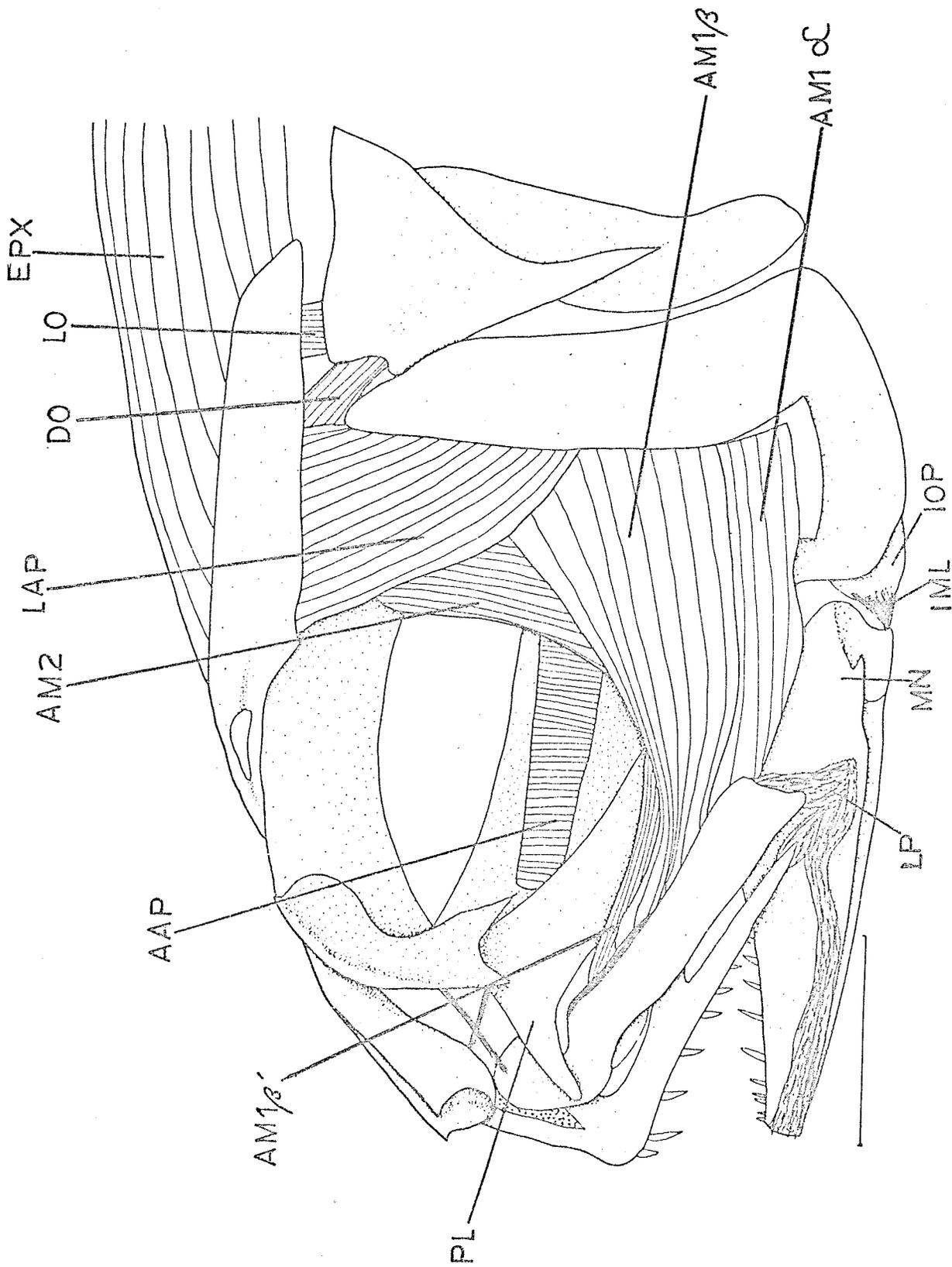


Figure 59. Lateral view of the superficial cheek muscles of Malacocephalus occidentalis, UMLL 25600, 49 mm HL.

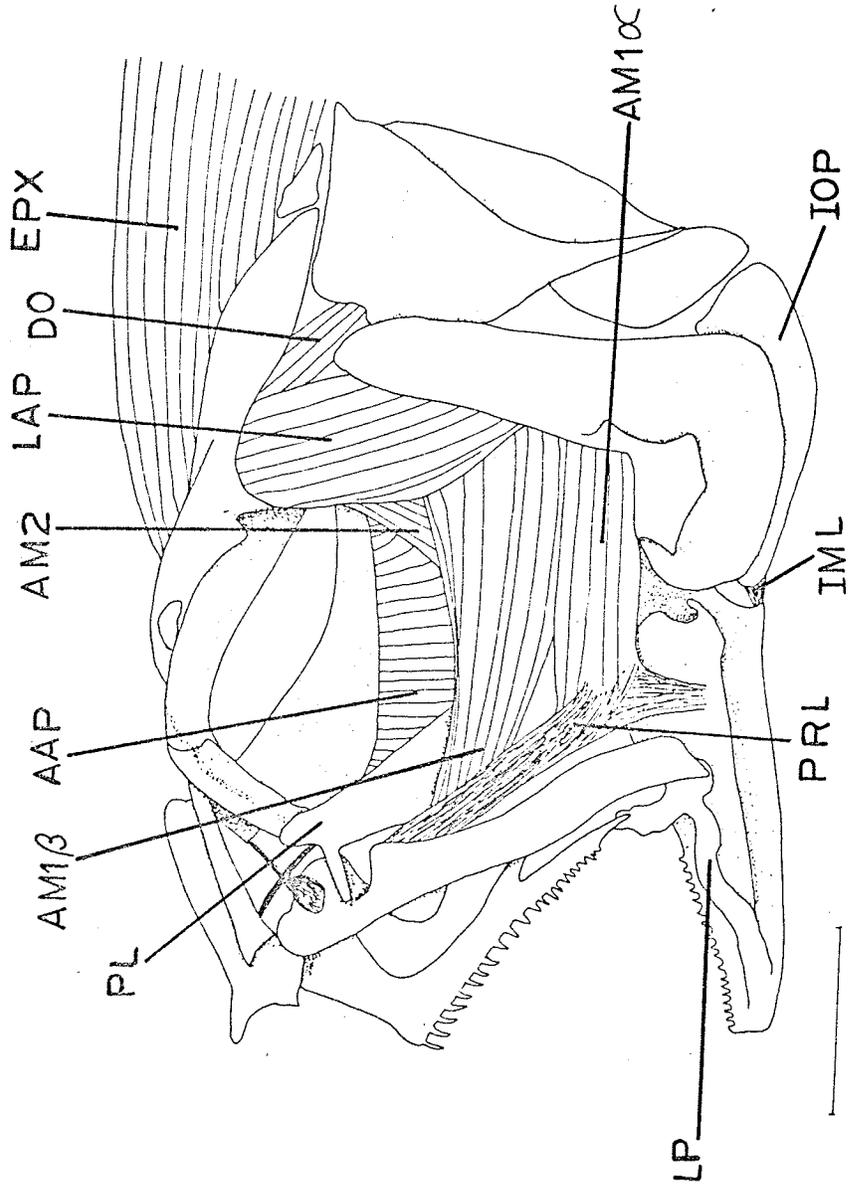


Figure 60. Lateral view of the superficial cheek muscles of Nezumia bairdii, MCZ 51176, 65 mm HL.

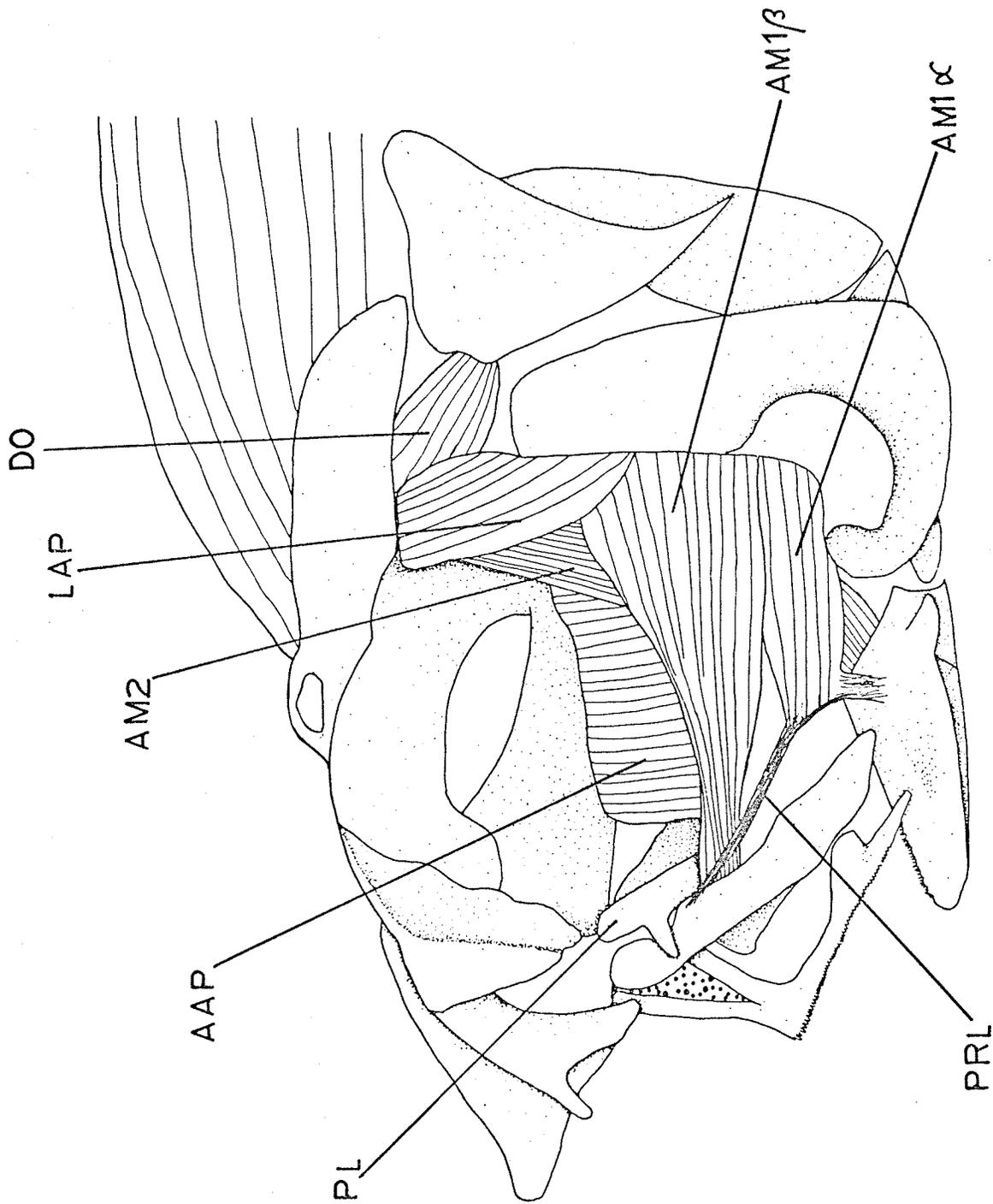
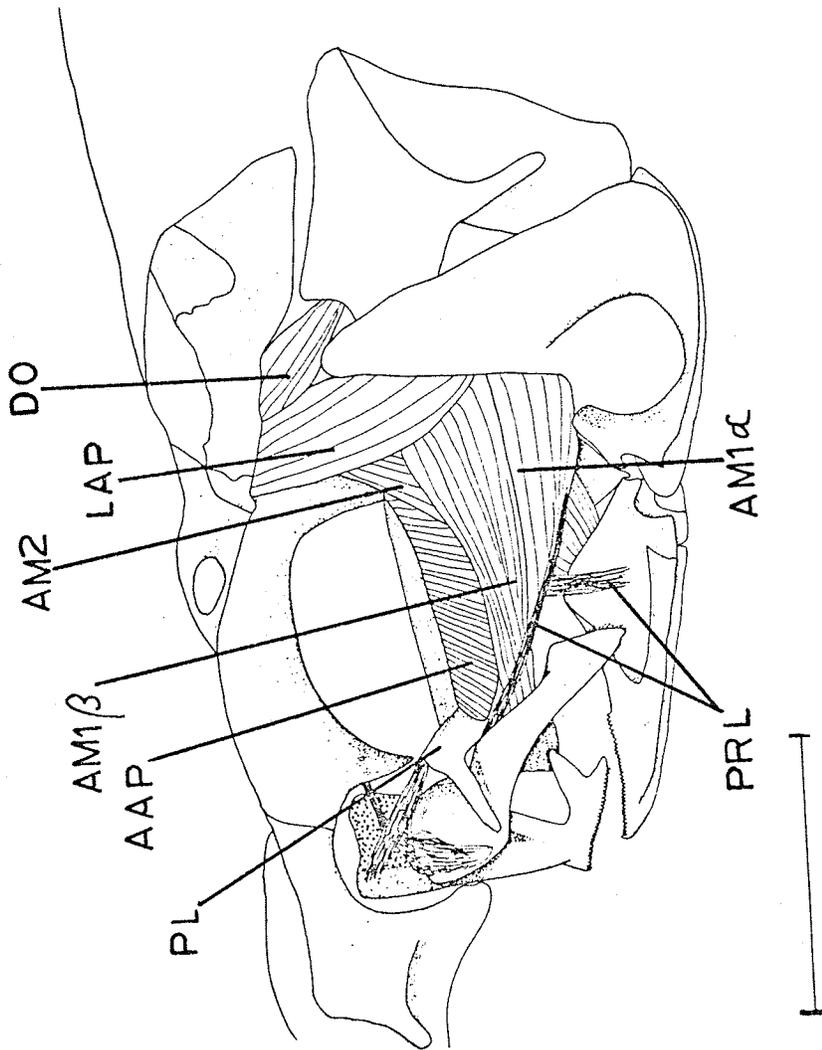


Figure 61. Lateral view of the superficial cheek  
muscles of Mataeocephalus acipenserinus, USNM 126542,  
50 mm HL.



posteriorly beyond the postmaxillary process. The maxilla of Mataeocephalus acipenserinus is wide and round anteriorly, with the premaxillary condyle large and removed from the articular process of the premaxilla posteriorly. The palatine groove is moderate and the primordial ligament process is shallow.

Coryphaenoides rupestris has long ascending processes of the premaxillae and fairly long alveolar processes (figure 62). The postmaxillary process originates halfway along the alveolar process and is broad posteriorly.

The maxilla in all species of Coryphaenoides examined is long and narrow posteriorly, with a pronounced premaxillary condyle and distinct primordial ligament process (figures 62 to 65).

The premaxilla of Coryphaenoides carapinus has moderate ascending processes, long alveolar processes and postmaxillary processes which are broad posteriorly (figure 63).

Coryphaenoides armatus has moderately long ascending processes and long alveolar processes (figure 64). The small postmaxillary process is near the distal end of the alveolar process.

Coryphaenoides acrolepis has relatively short ascending processes of the premaxilla, long alveolar processes and sharp, thin postmaxillary processes.

The premaxilla of Coryphaenoides leptolepis has a moderate ascending process, a long alveolar process and a small,

Figure 62. Lateral view of the superficial cheek muscles of Coryphaenoides rupestris, VIMS 00899, 82 mm HL.

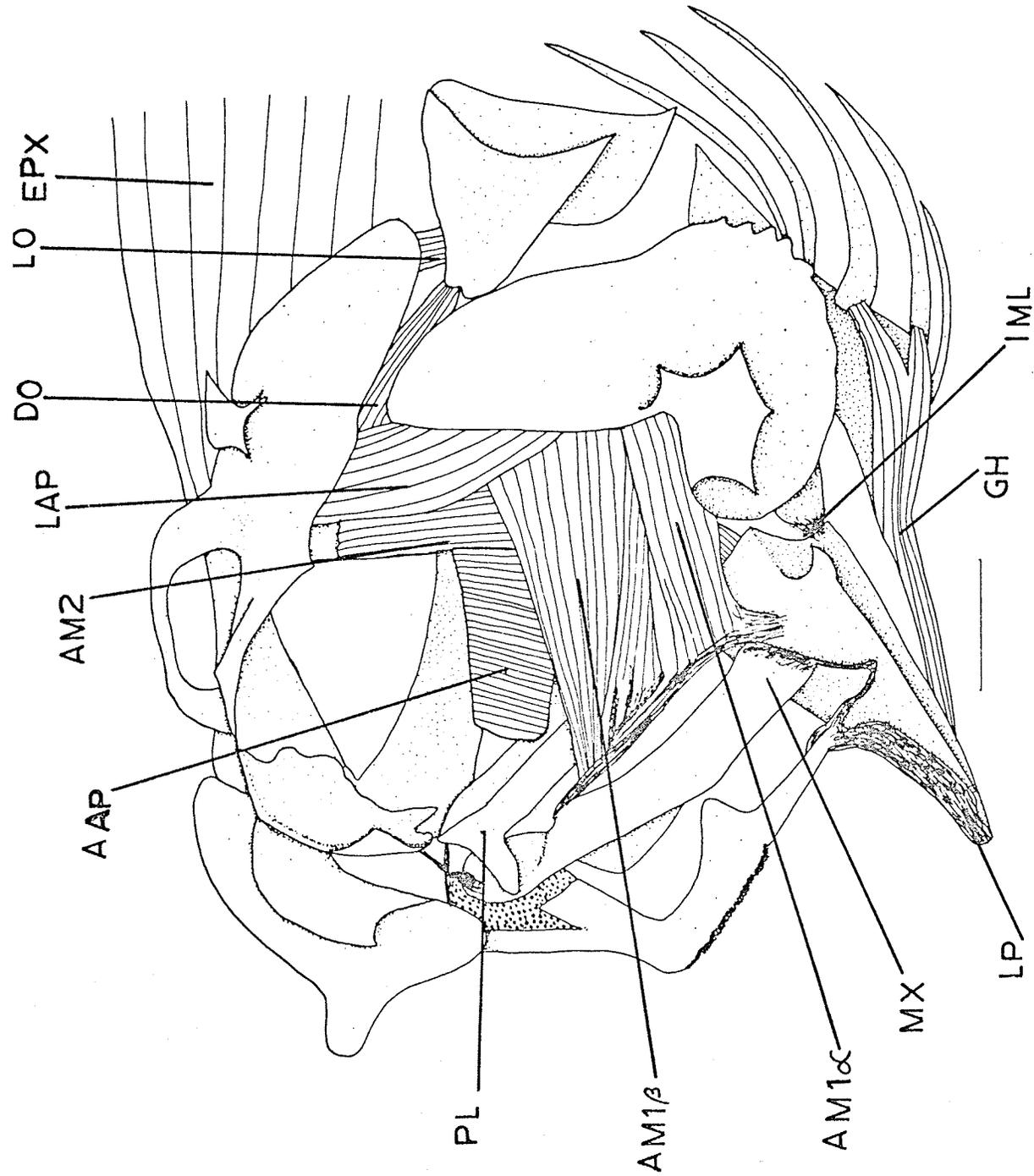


Figure 63. Lateral view of the superficial cheek muscles of Coryphaenoides carapinus, MCZ 51864, 54 mm HL.

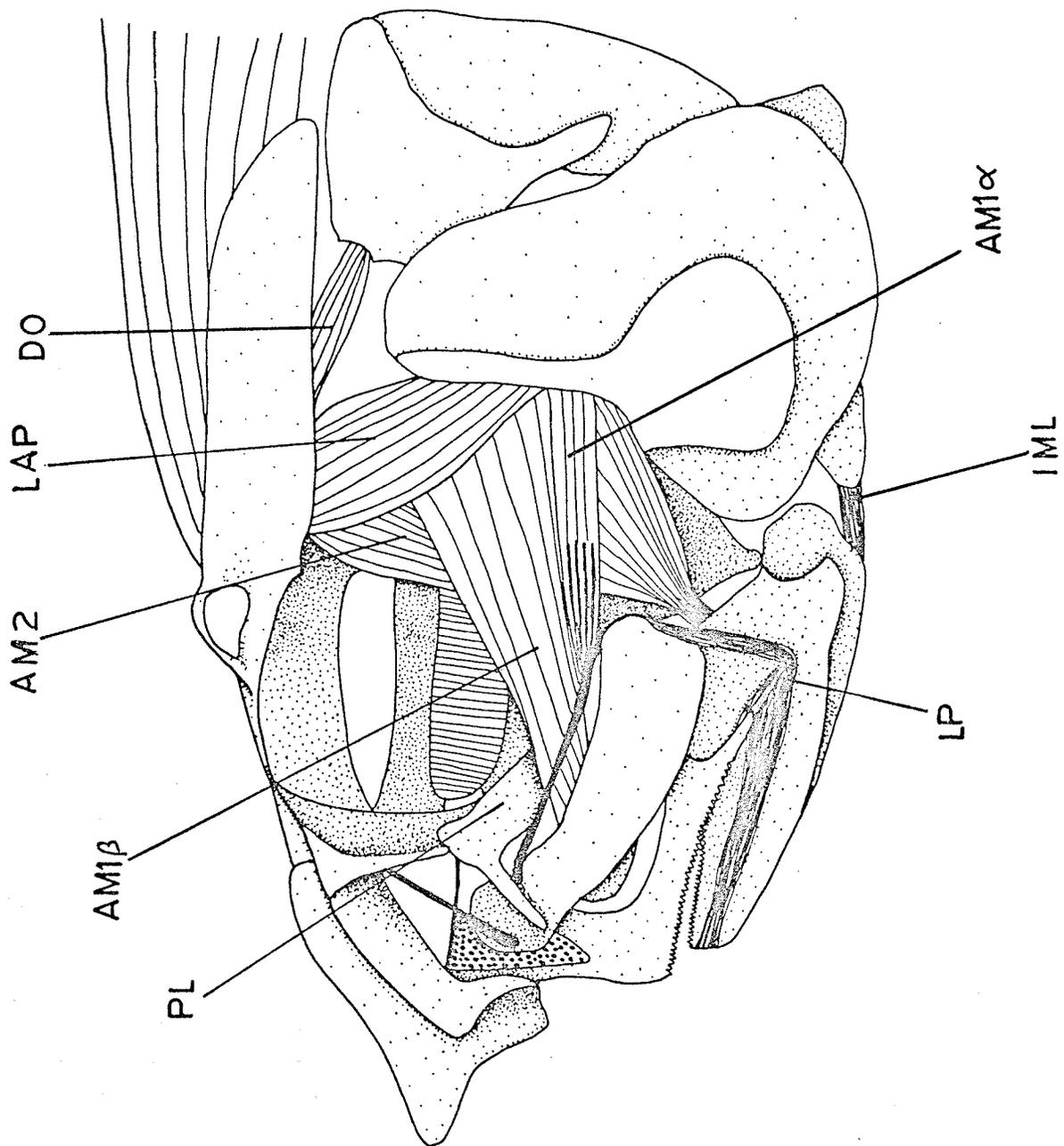


Figure 64. Lateral view of the superficial cheek  
muscles of Coryphaenoides armatus, MCZ 51868,  
78 mm HL.

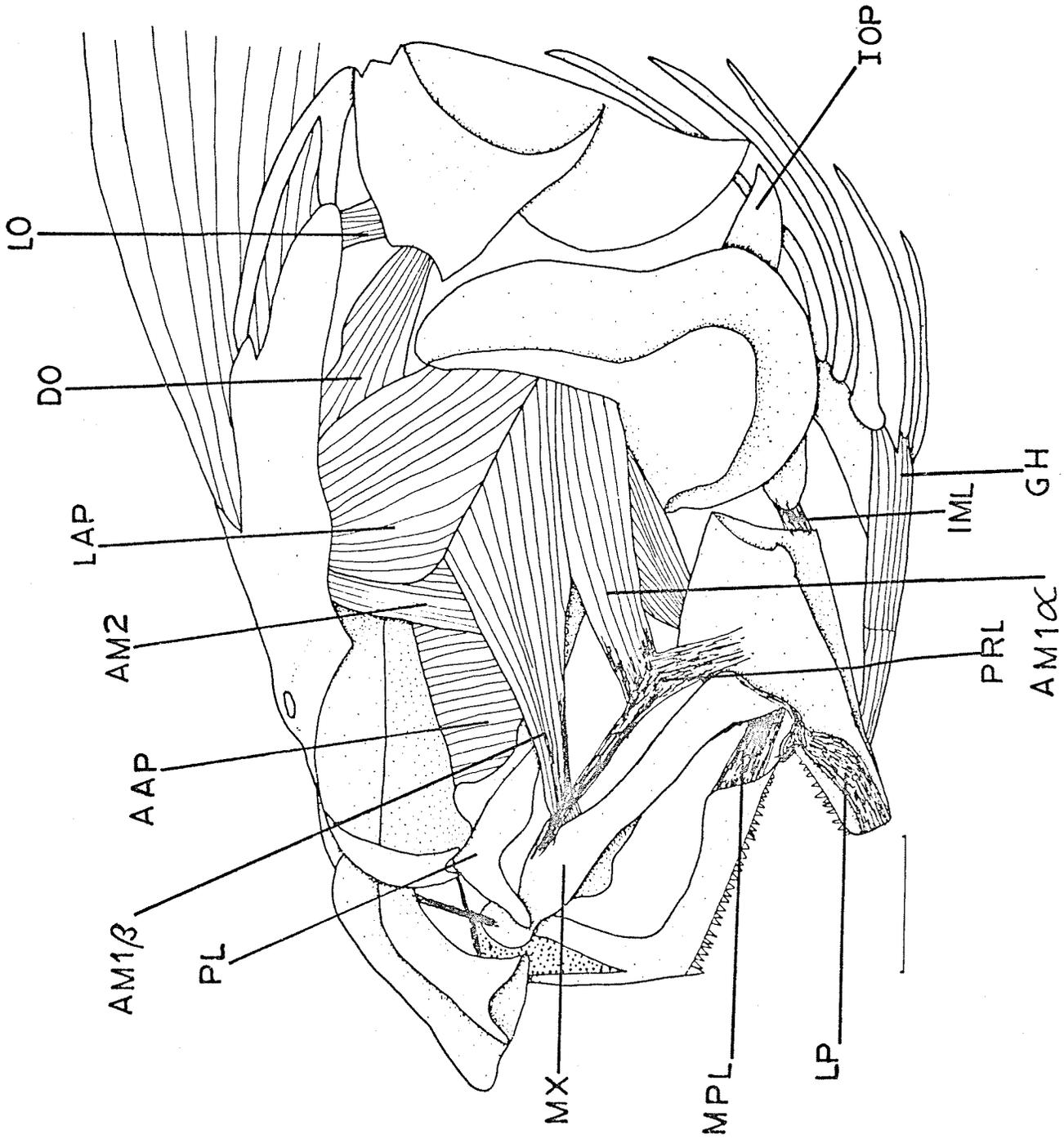
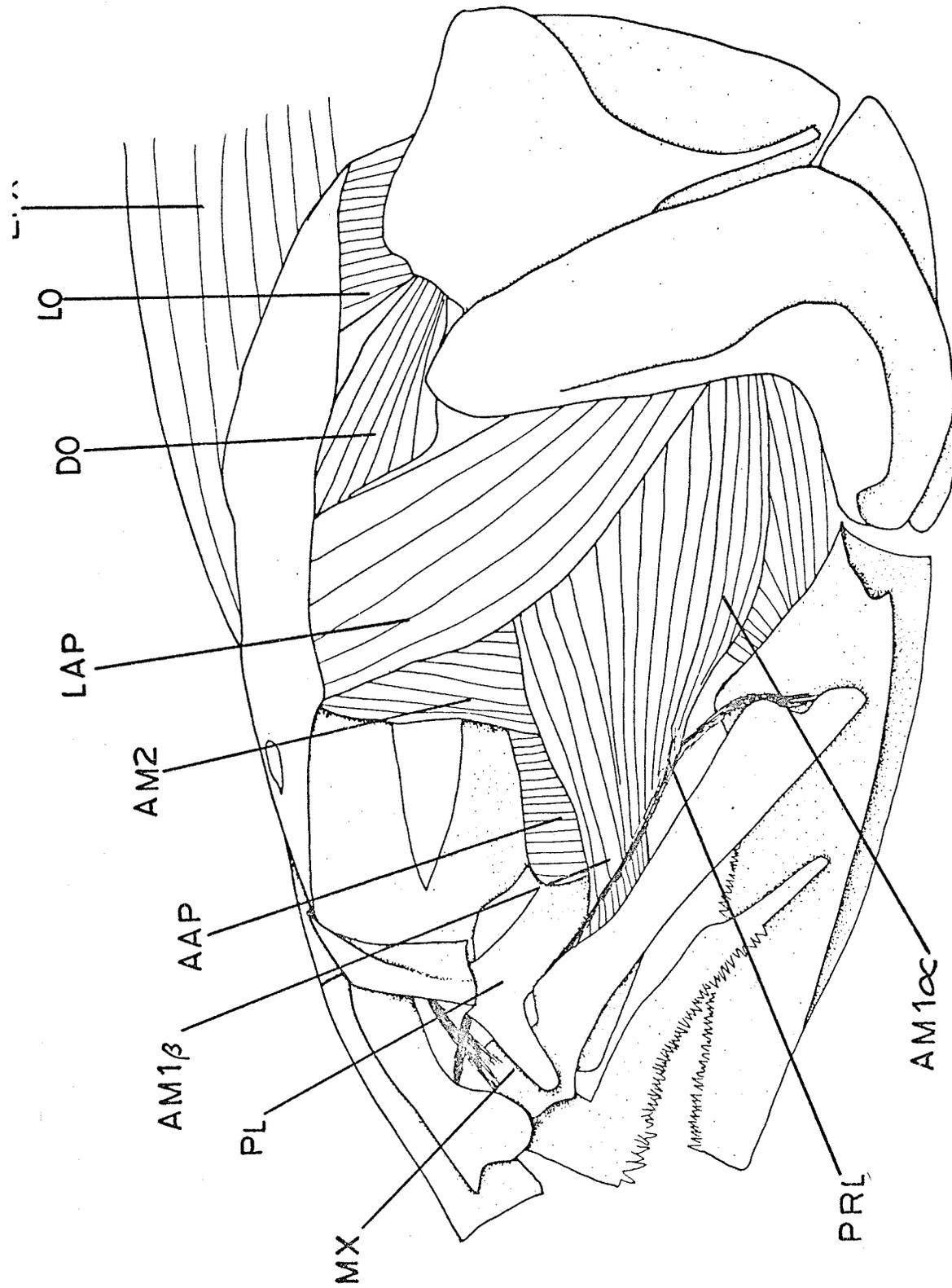


Figure 65. Lateral view of the superficial cheek muscles of Coryphaenoides pectoralis, MCZ 51930, 110 mm HL.



triangular postmaxillary process that is halfway along the alveolar process (figure 35).

The premaxillae of Coryphaenoides pectoralis differ from those of the other species of Coryphaenoides in having very short ascending processes, long alveolar processes and only a small dorsal rise in the alveolar process at the place where the postmaxillary process is in most (figure 65).

Macrourus berglax (figure 5), Abyssicola macrochir (figure 66) and Coelorinchus species (figures 67 to 72) share a number of features of the premaxilla. All have long ascending processes, and with the exception of A. macrochir, the alveolar process is short. There is a substantial postmaxillary process in all of them; in Coelorinchus coelorinchus carminatus, C. chilensis and C. japonicus the postmaxillary process extends posteriorly farther than the alveolar process.

The maxilla of Macrourus berglax has a large, wide premaxillary condyle and a high primordial ligament process (figure 5).

Abyssicola macrochir has a long maxilla with a large premaxillary condyle, shallow palatine groove and small primordial ligament process (figure 66).

In all species of Coelorinchus examined, the maxilla has a wide head with a high primordial ligament process and moderate groove for the palatine. The ramus of the maxilla is narrow posteriorly in C. chilensis and C. innotabilis (figures 68 and 71), and wider in the other species.

Figure 66. Lateral view of the superficial cheek  
muscles of Abyssicola macrochir, USNM 77248, 75 mm HL.

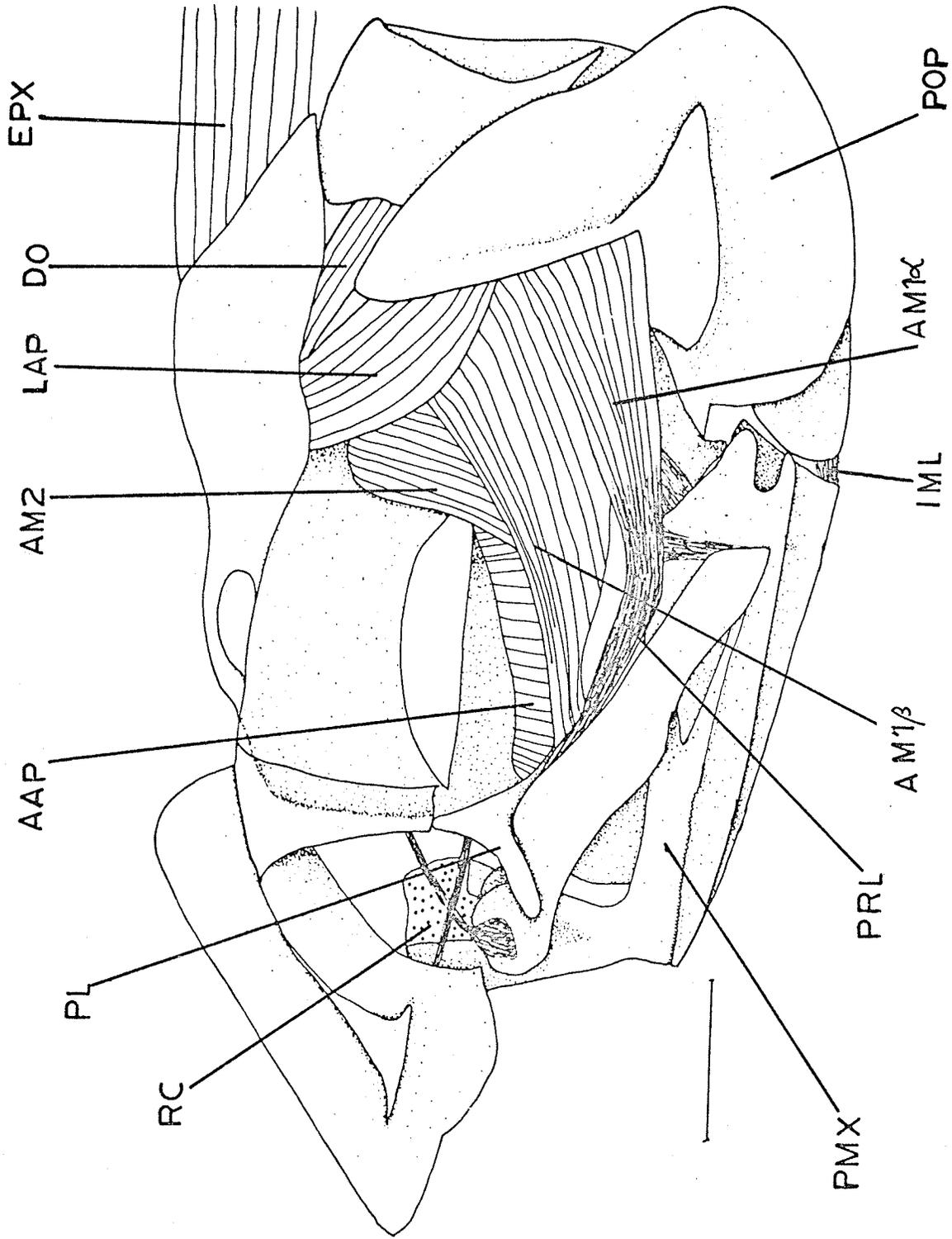


Figure 67. Lateral view of the superficial cheek muscles of Coelorinchus coelorinchus carminatus, UMML 13169, 66 mm HL.

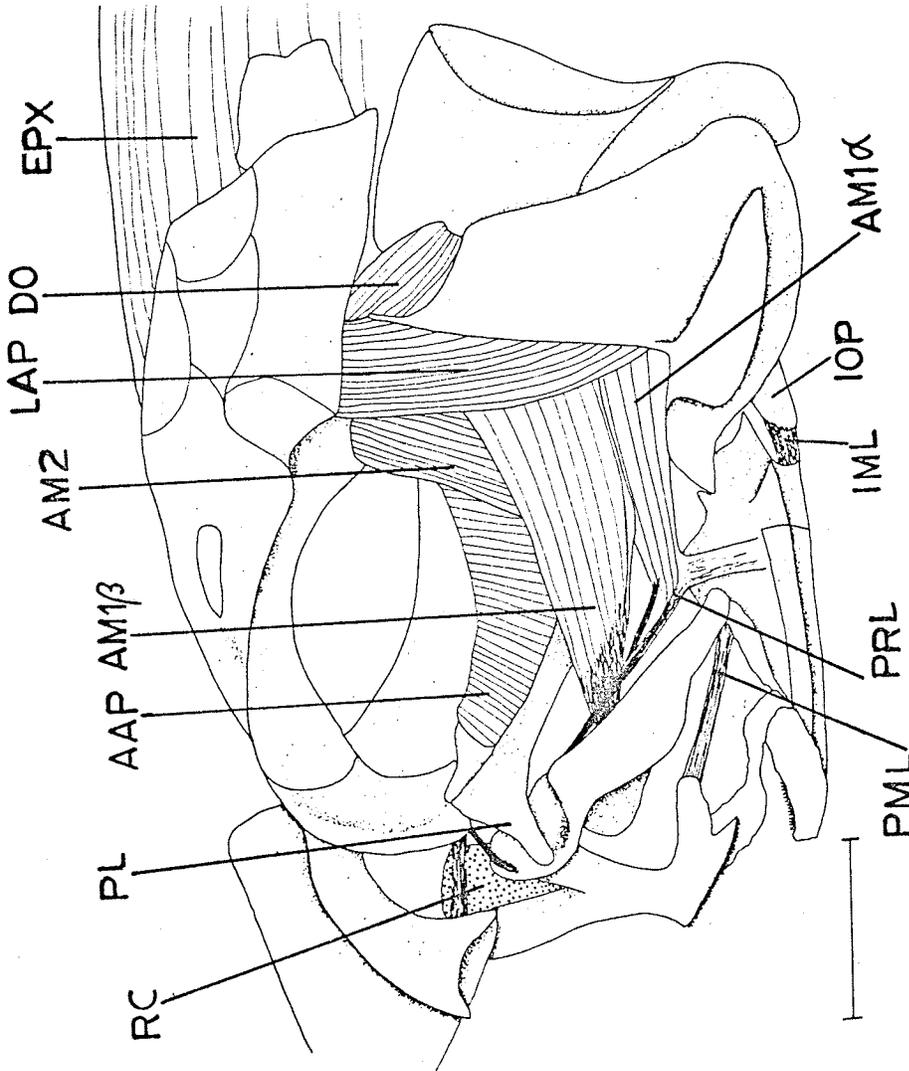


Figure 68. Lateral view of the superficial cheek muscles of Coelorinchus chilensis, LACM Eltanin 1989, 43 mm HL.

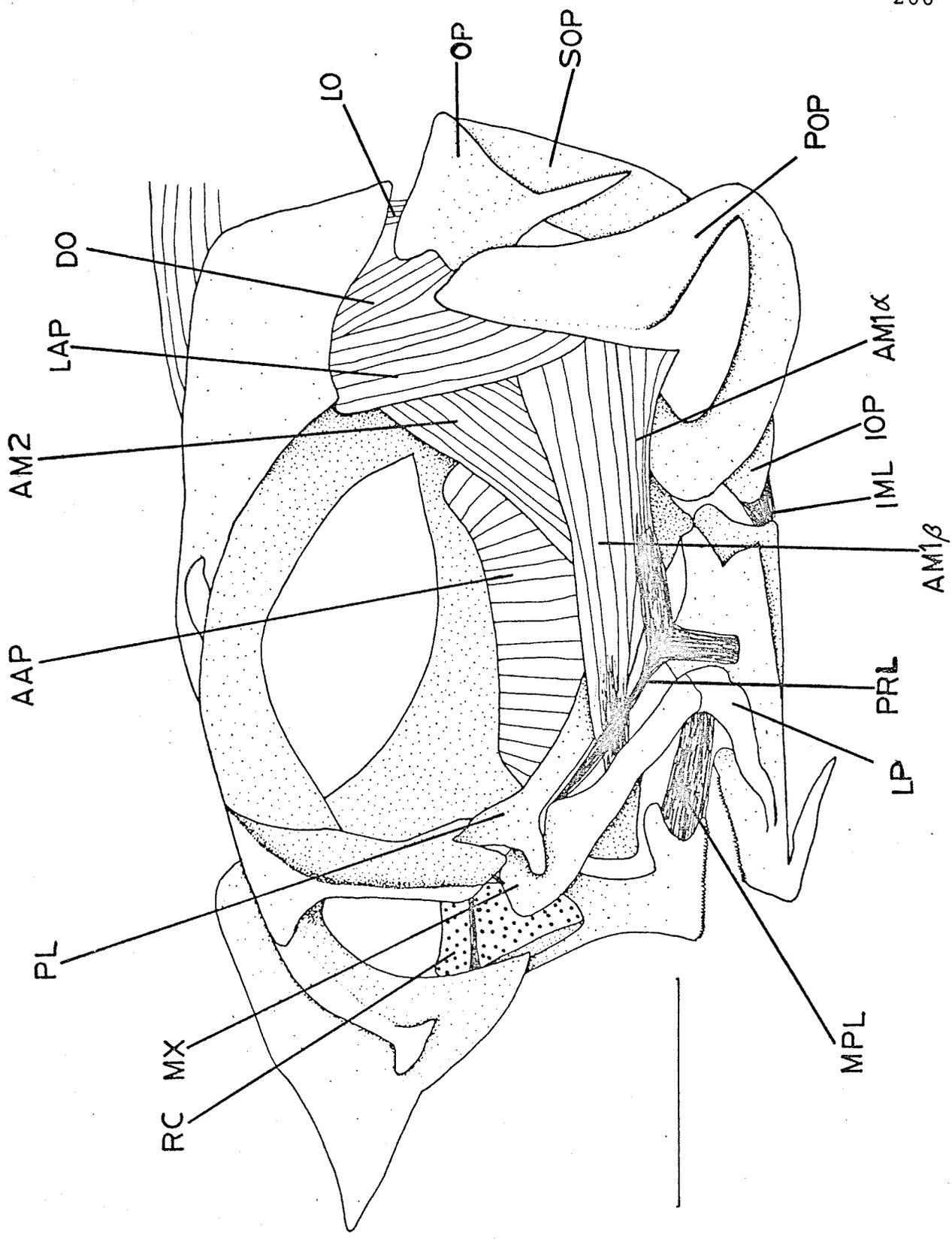


Figure 69. Lateral view of the superficial cheek muscles of Coelorinchus occa, UML 26794, 133 mm HL.

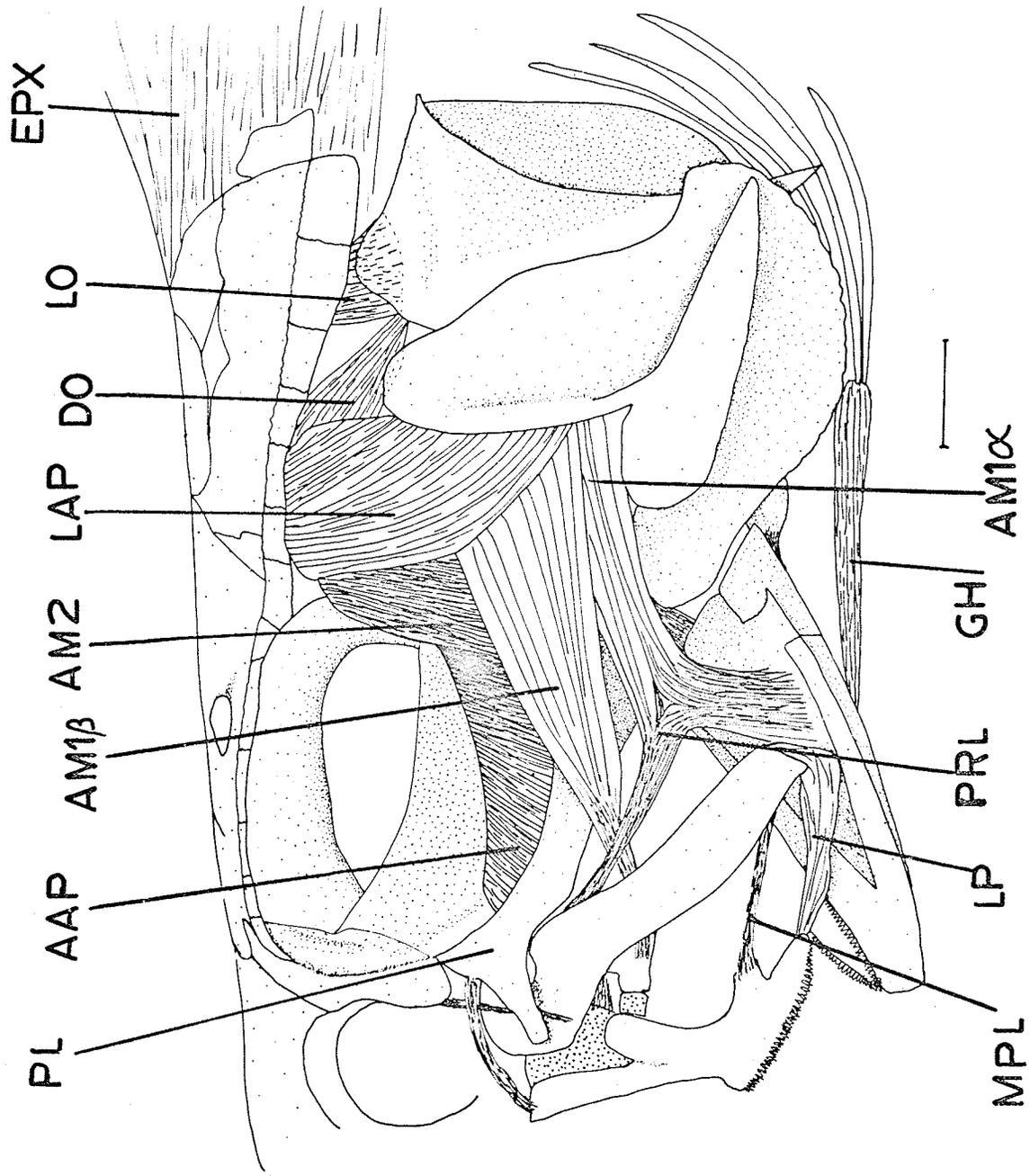


Figure 70. Lateral view of the superficial cheek  
muscles of Coelorinchus jordanii, USNM 77197, 51 mm HL.

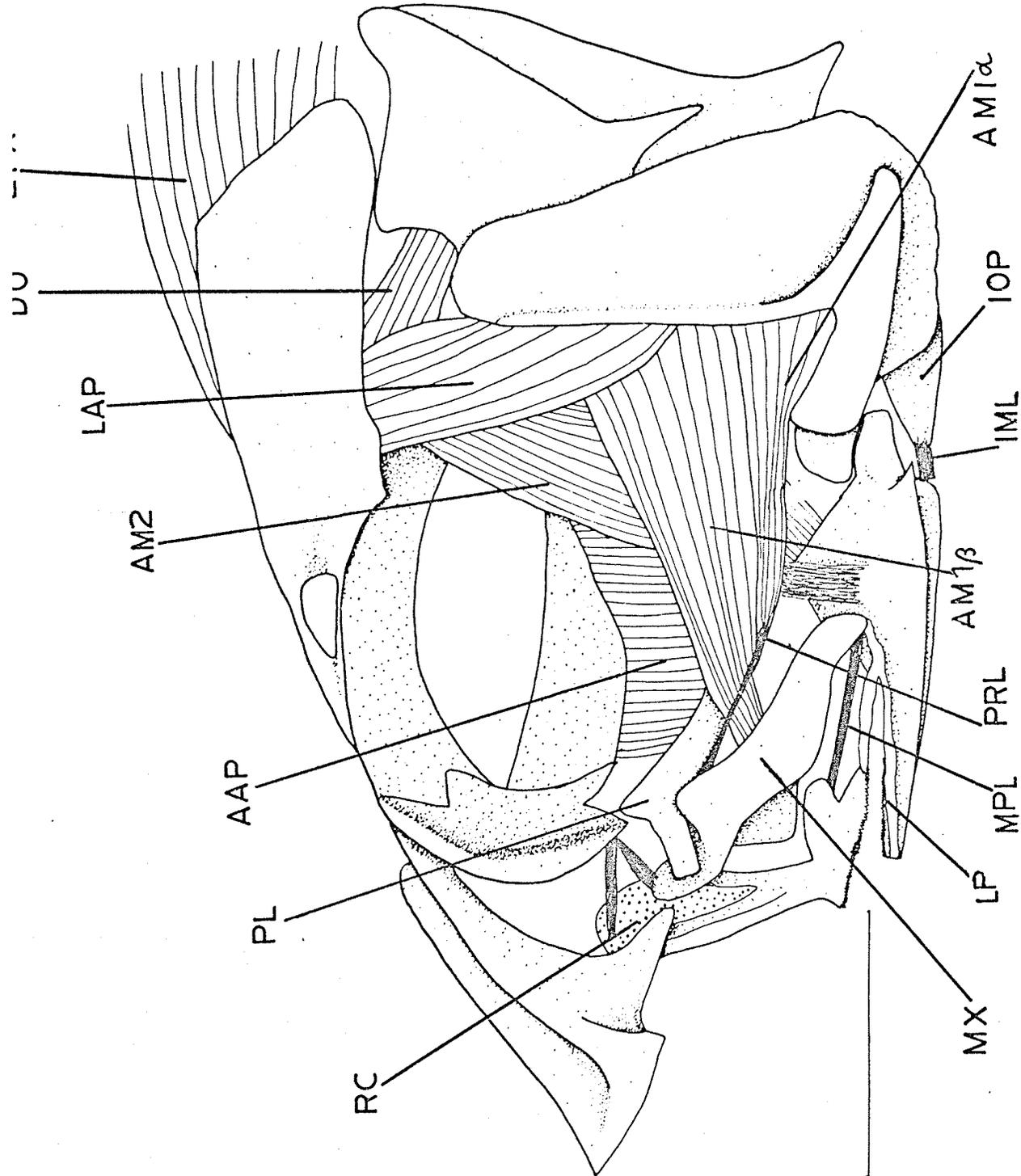


Figure 71. Lateral view of the superficial cheek muscles of Coelorinchus innotabilis, LACM Eltanin 1718, 54 mm HL.

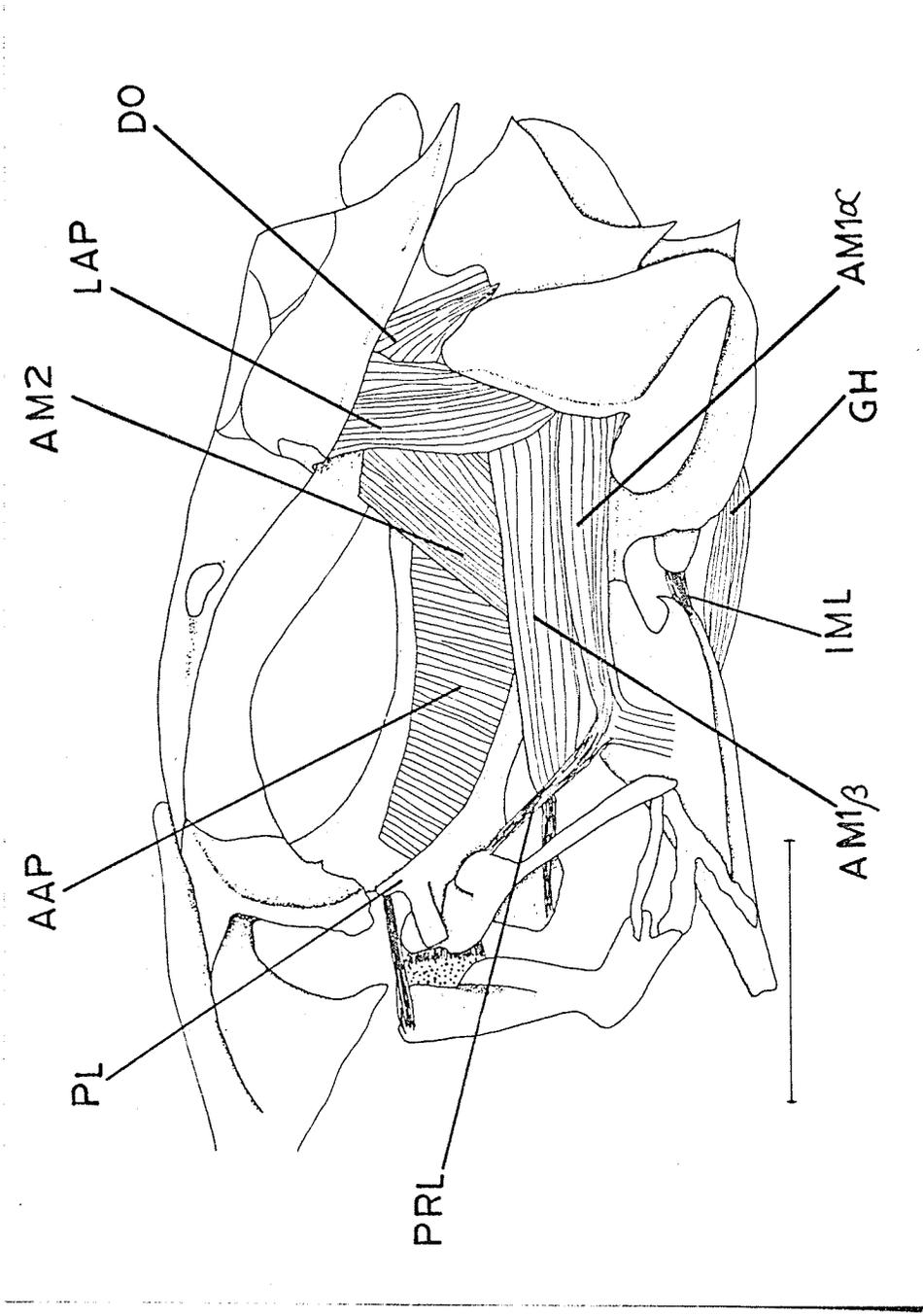
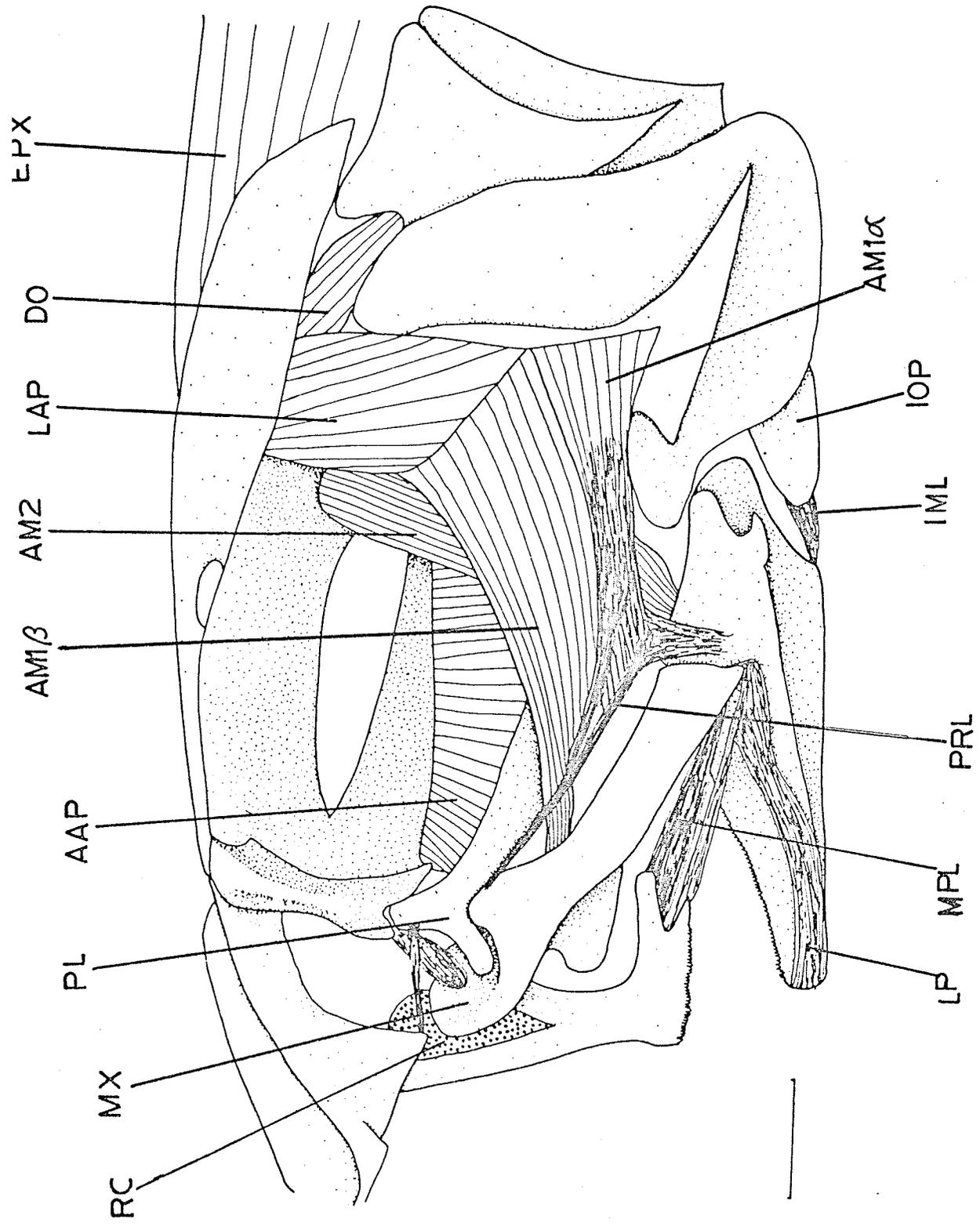


Figure 72. Lateral view of the superficial cheek  
muscles of Coelorinchus japonicus, SU 7939, 121 mm HL.



The premaxillae of Trachyrincus helolepis have short ascending processes and very long alveolar processes (figures 73 and 97A). There is a long, thin postmaxillary process. The maxilla is very long and narrow with a long premaxillary condyle and a shallow rise at the insertion of adductor mandibulae 1  $\alpha$ . The head of the maxilla is at a sharp angle dorsally relative to the part posterior to the palatine articulation.

#### VII. Hyoid Apparatus

There is little variation in the morphology of the hyoid in the fishes considered here. In those with dorsoventrally depressed heads and small mouths the hyoid is shorter and broader than in those with more laterally compressed heads (Okamura, 1970b, pages 83-88).

#### VIII. Pharyngeal Jaws

The pharyngeal teeth of several species of macrourids have been described by Geistdorfer (1972). Okamura (1970b, pages 19 to 24) has described the structure of gill rakers and occlusion of the first gill slit in many species. All species of macrourines have tissue that restricts the first gill slit, and this occlusion is the greatest in Coelorinchus.

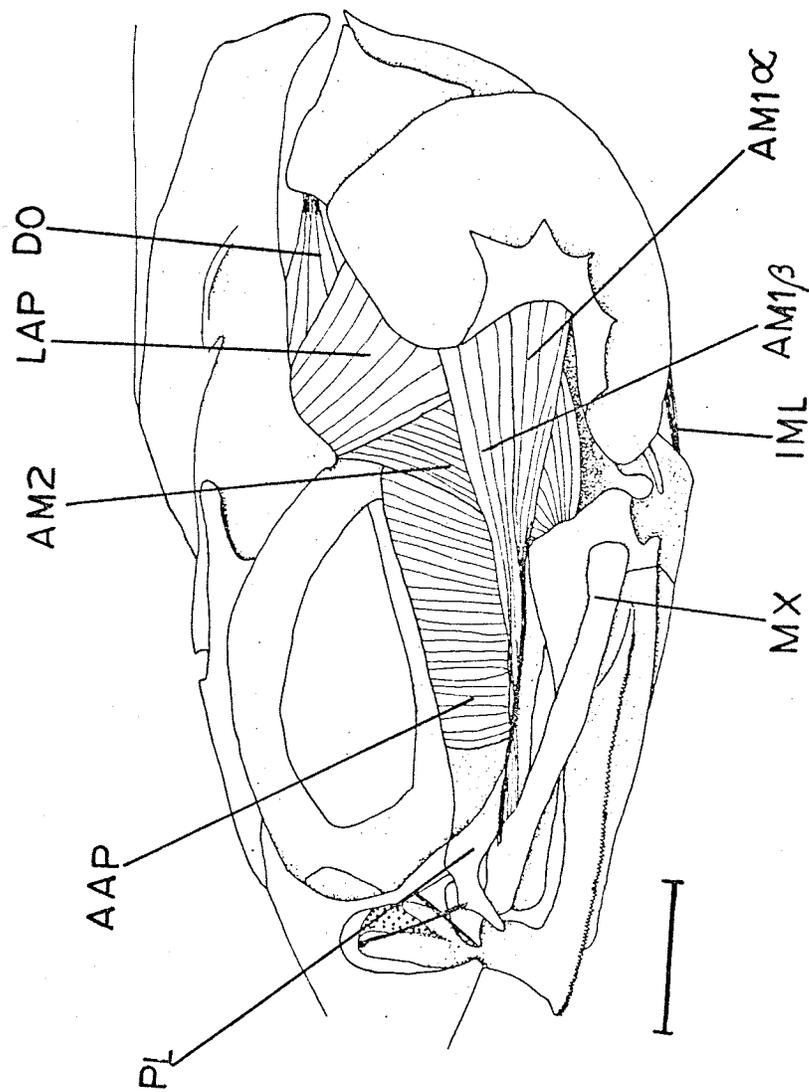
The pharyngeal muscles of Coelorinchus occa are illustrated in figure 8.

#### IX. Muscles of the Head

##### A. Muscles Between Suspensorium and Jaws

The adductor mandibulae complex of muscles runs from the suspensorium to the maxilla and to the mandible. There

Figure 73. Lateral view of the superficial cheek muscles of Trachyrincus helolepis, SOSC Reg. No. 309, 98 mm HL.



are two major subsections, adductor mandibulae 1  $\alpha$  and adductor mandibulae 1  $\beta$ , that run anteriorly from the preopercle to the maxilla, and one main section, adductor mandibulae 2, that runs ventrally from the metapterygoid to insert on a small section, adductor mandibulae  $\omega$ , inside the lower jaw. Subsection Al $\alpha$  inserts on the primordial ligament, which extends from the maxilla just posterior to the palatine articulation to the mandible, running medial to the distal end of the maxilla. In Macruronus novazelandiae, Steindachneria argentea and Bathygadus macrops Al $\alpha$  has a long tendon anteriorly that inserts on the primordial ligament close to its attachment to the maxilla (figures 55,56 and 57). In the species examined belonging to the subfamily Macrourinae, Al $\alpha$  has a short, broad tendon that inserts directly anterior to the muscle near the ascending process of the mandible. There is a distinct process on the maxilla at the point where the primordial ligament inserts in the macrourines (figures 58 to 72). Part of the tendonous insertion of Al $\alpha$  includes a small tendon from the dorsal part of the muscle to the primordial ligament about halfway between the insertion of the rest of the muscle and the attachment to the maxilla in Coryphaenoides rupestris (figure 62), Coelorinchus coelorinchus carminatus (figure 67) and Coelorinchus japonicus (figure 72).

The adductor mandibulae 1  $\beta$  of macrourids has been described previously by Rosen and Patterson (1969, pages

423 and 428) as the levator maxillae superioris. It lies dorsal, and sometimes also medial, to  $A1\alpha$  and inserts muscoulously on the medial surface of the premaxillary condyle or just posterior to this condyle (figure 97). Its origin is medial to the levator arcus palatini and lateral to adductor mandibulae 2 in most species.

In Macruronus novaezelandiae  $A1\beta$  originates tendonously on the metapterygoid medial to A2 and is small posteriorly and widens anterior to the orbit (figure 74).  $A1\beta$  in Steindachneria argentea originates lateral to A2 and is a very thin, broad layer posteriorly and narrow anteriorly (figure 75). In Bathygadus macrops this muscle has the same origin as in S. argentea, and is a larger muscle curving ventrally around the orbit and dorsally again before its insertion on the primordial ligament (figure 76).

In the macrourines there is a small, medial section of  $A1\beta$ , denoted as  $A1\beta'$ , that originates tendonously on the metapterygoid, runs through the fibers of A2 and inserts on the maxilla with  $A1\beta$  (figures 78-82). It was not found in Mataeocephalus acipenserinus, Coryphaenoides carapinus, Coelorinchus innotabilis and Macrourus berglax. The first three of these are small and the muscle may have been missed because of its small size.

The two subsections of adductor mandibulae 1 are similar in all species of macrourines examined. They are particularly long and narrow in Coelorinchus chilensis (figure 68), Coelo-

Figure 74. Lateral view of the deep cheek muscles of  
Macruronus novaezelandiae, MCZ 51164, 41 mm HL.

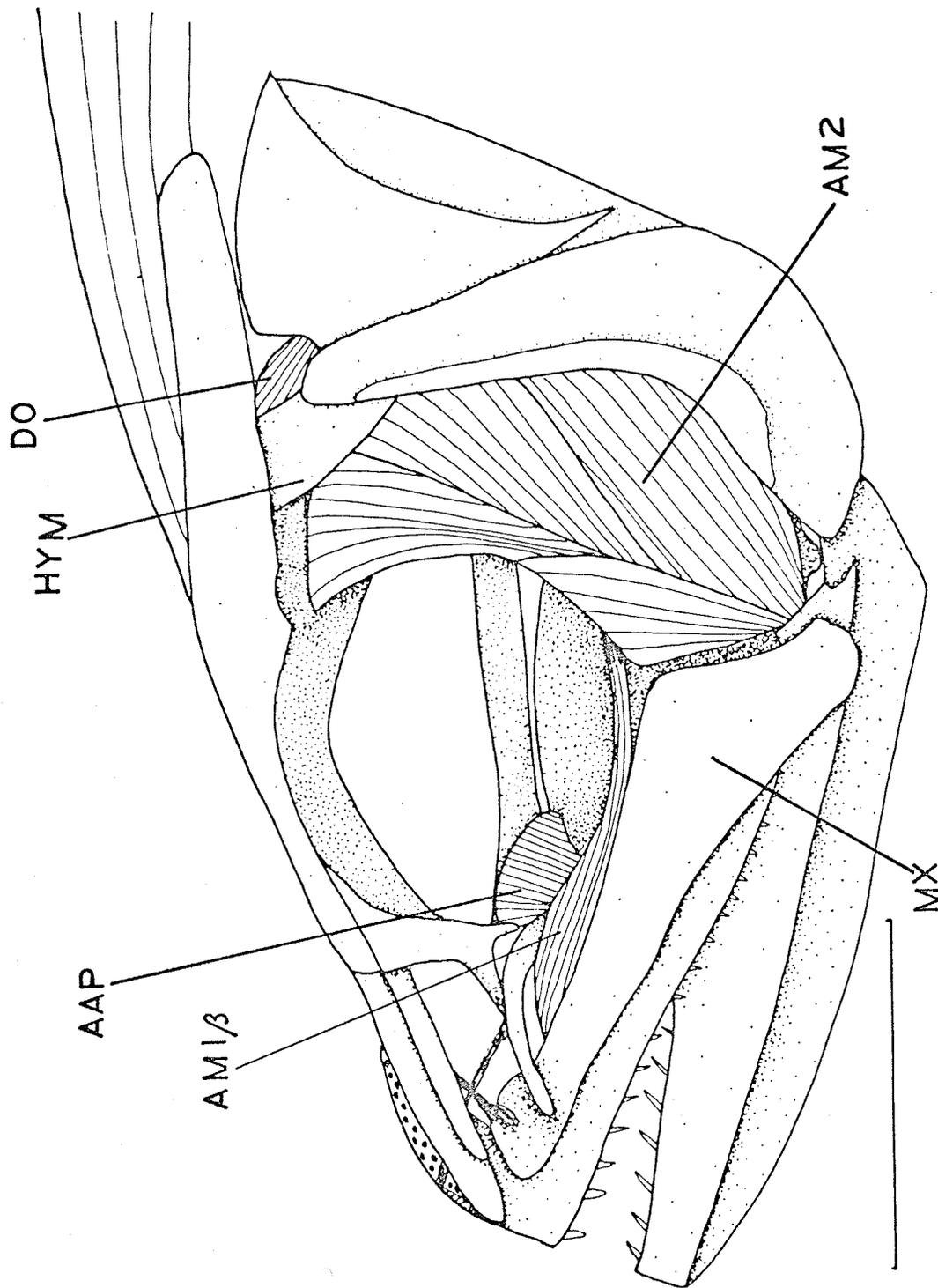


Figure 75. Lateral view of the deep cheek muscles  
of Steindachneria argentea, USNM 188852, 37 mm HL.

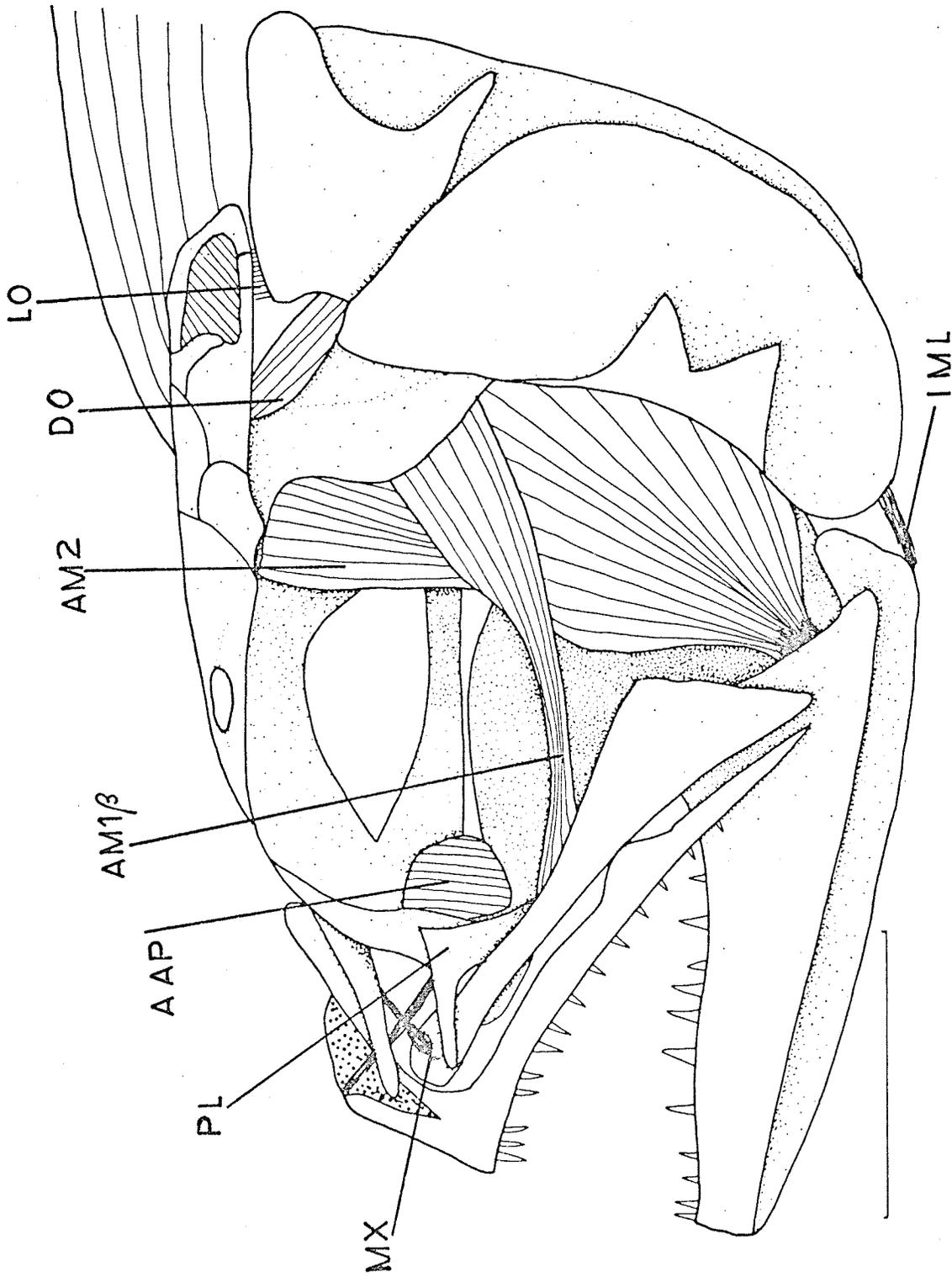


Figure 76. Lateral view of the deep cheek muscles  
of Bathygadus macrops, UMML 15193, 68 mm HL.

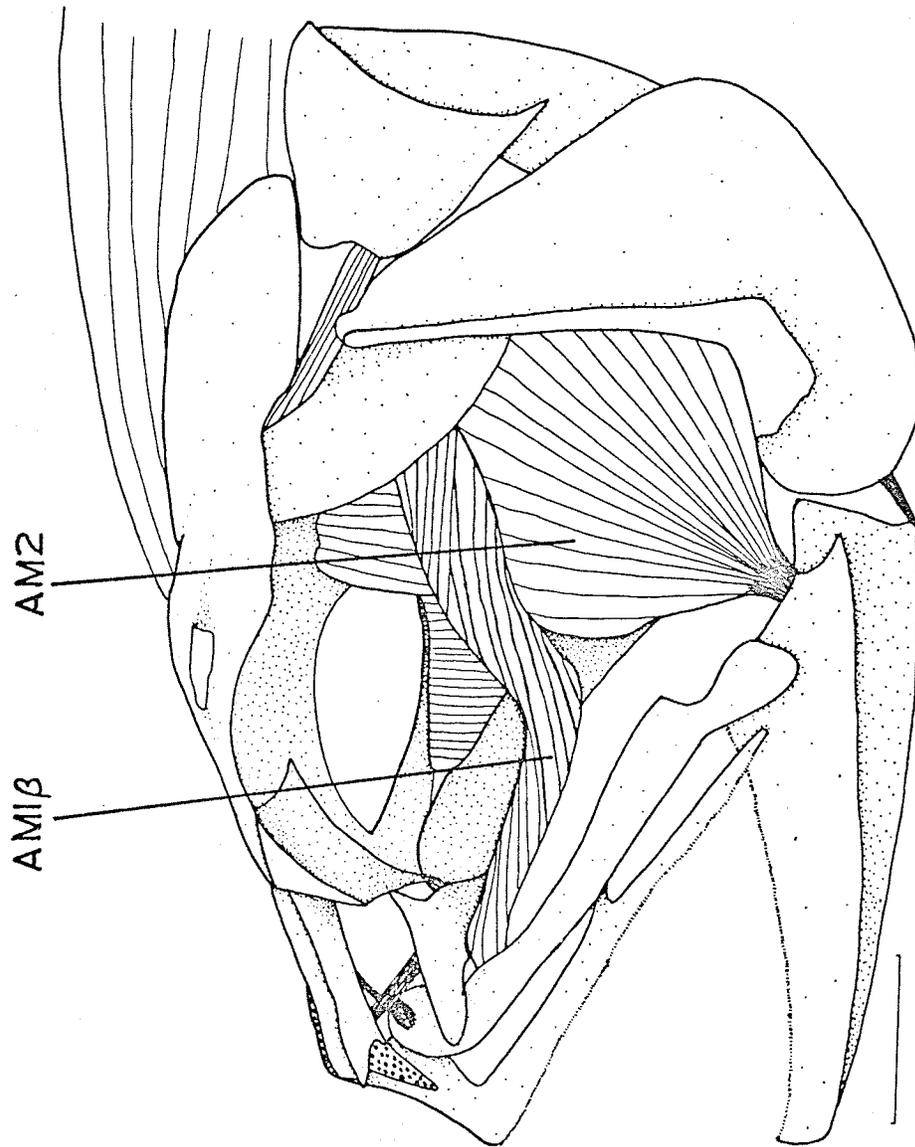


Figure 77. Lateral views of the deep cheek muscles  
of Lepidorhynchus denticulatus, MCZ 51515, 57 mm HL.

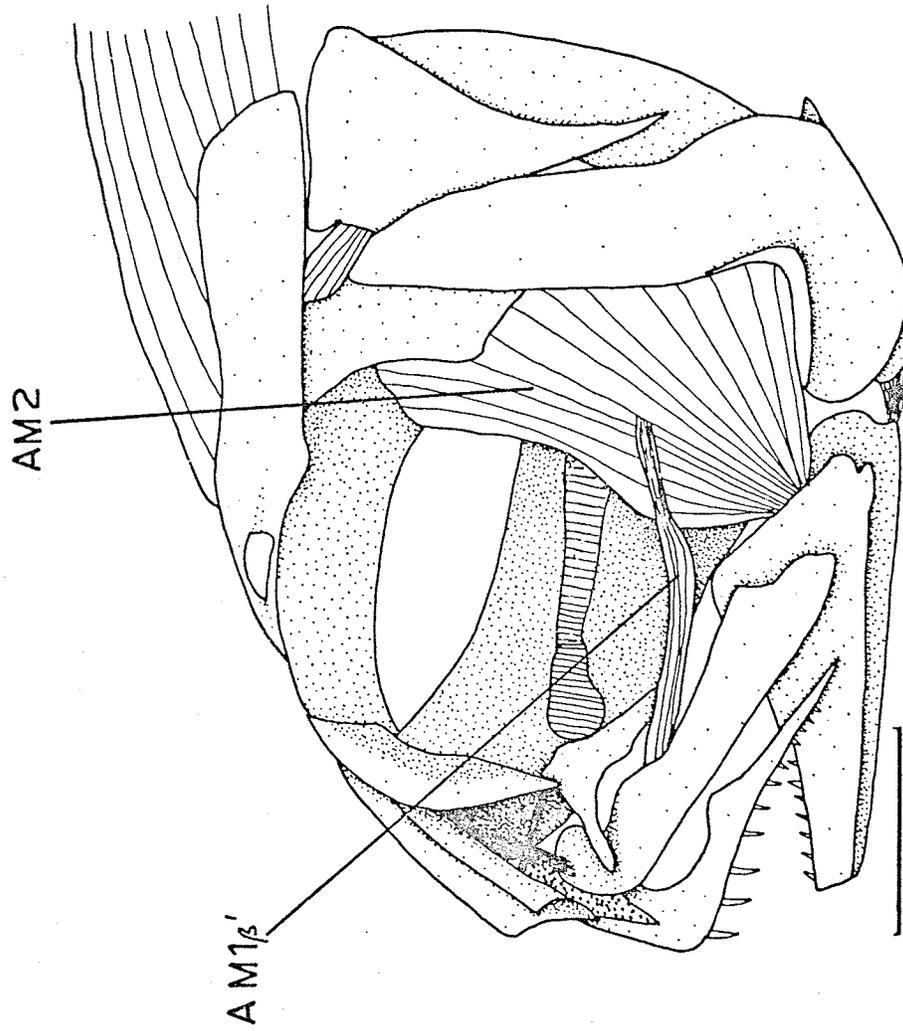


Figure 78. Lateral view of the deep cheek muscles of Malacocephalus occidentalis, UMML 25600, 51 mm HL.

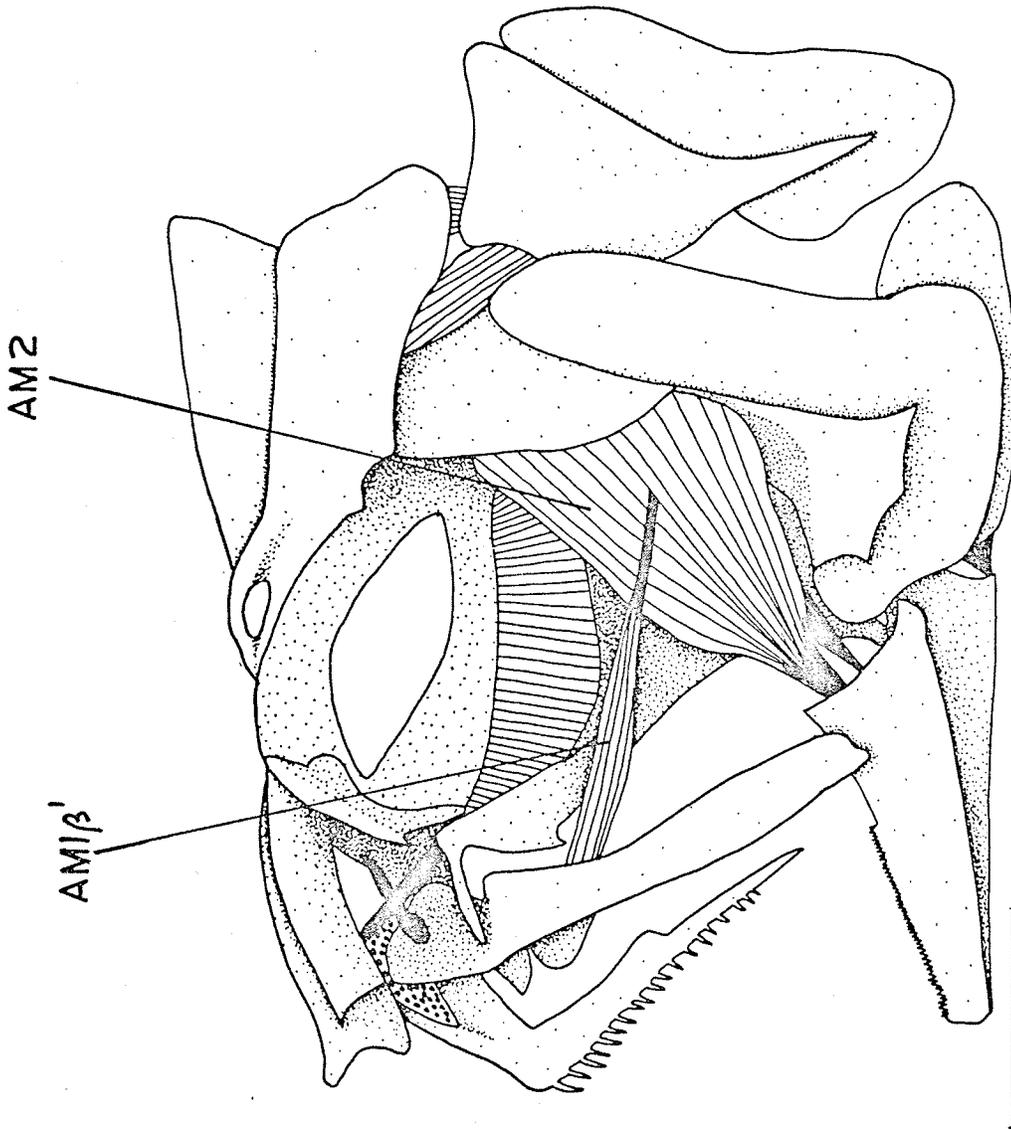


Figure 79. Lateral view of the deep cheek muscles  
of Nezumia bairdii, MCZ 51176, 65 mm HL.

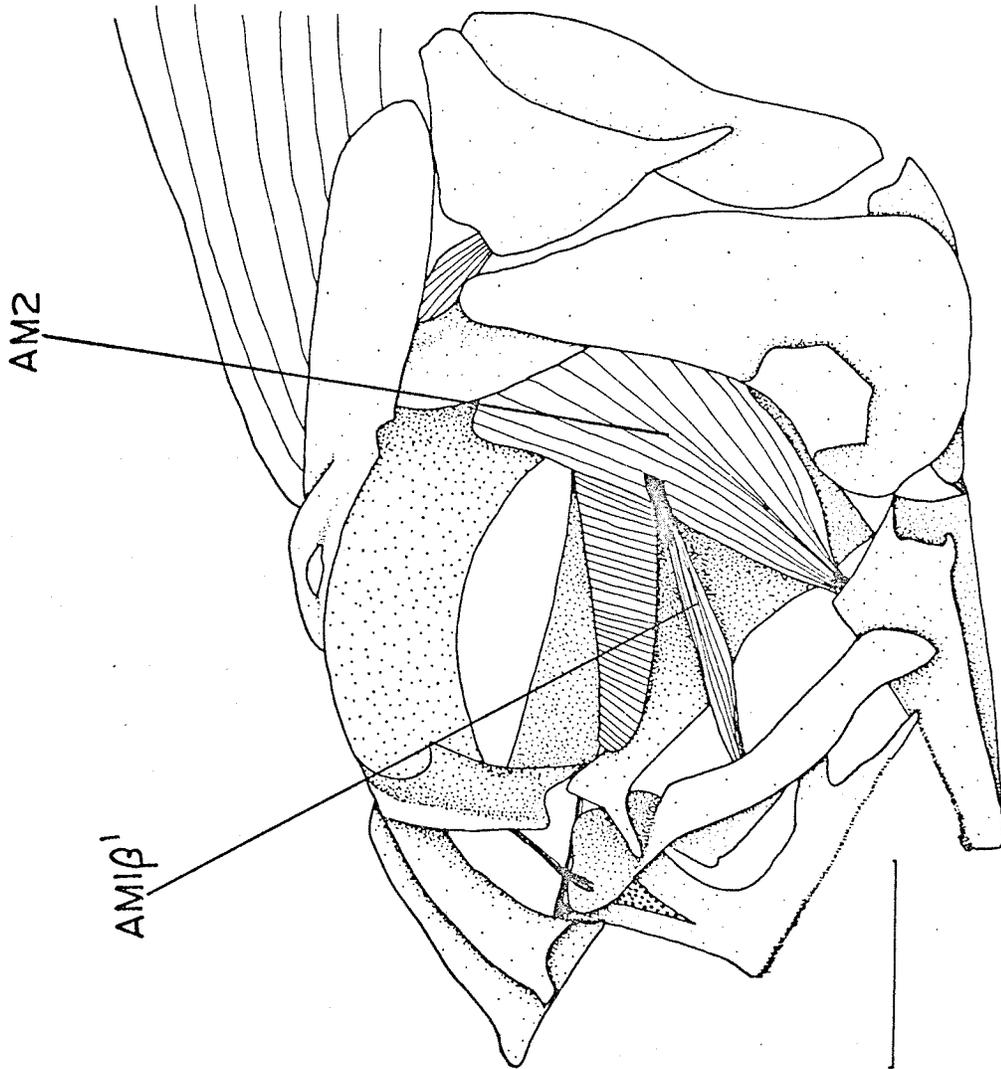


Figure 80. Lateral view of the deep cheek muscles  
of Coryphaenoides armatus, MCZ 51868, 78 mm HL.

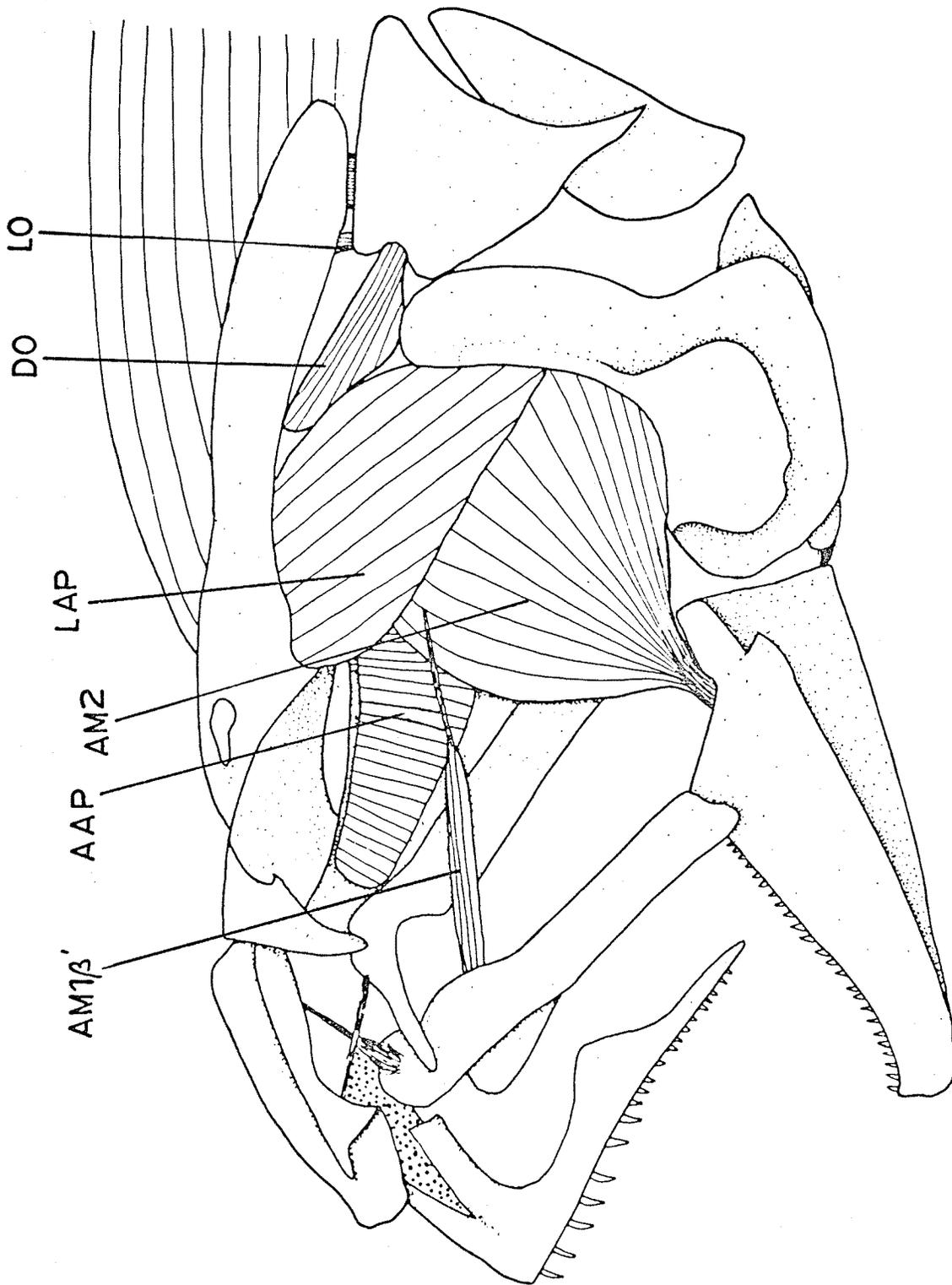


Figure 81. Lateral view of the deep cheek muscles  
of Abyssicola macrochir, USNM 77248, 75 mm HL.

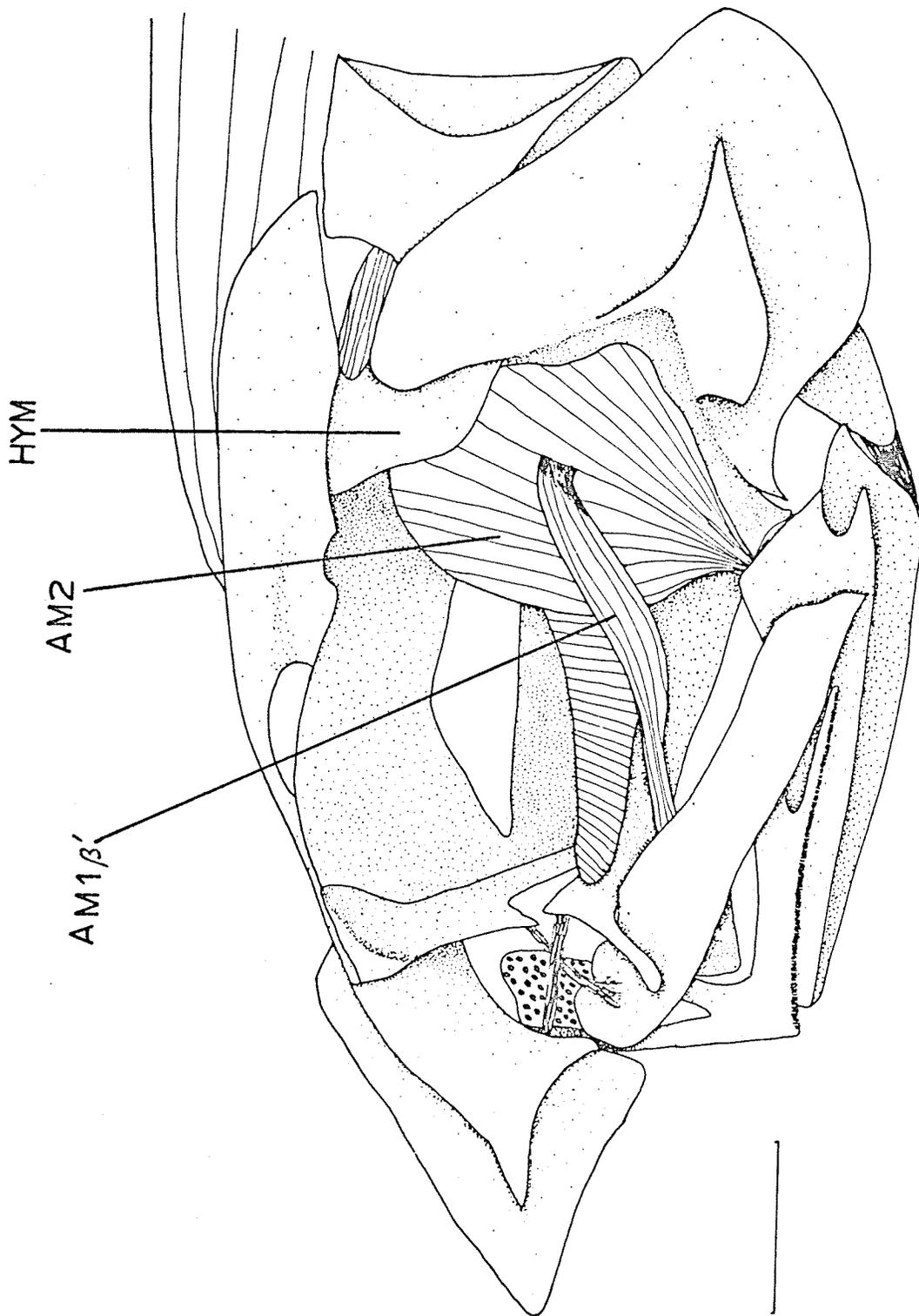


Figure 82. Lateral view of the deep cheek muscles  
of Coelorinchus occa, UMML 26794, 133 mm HL.

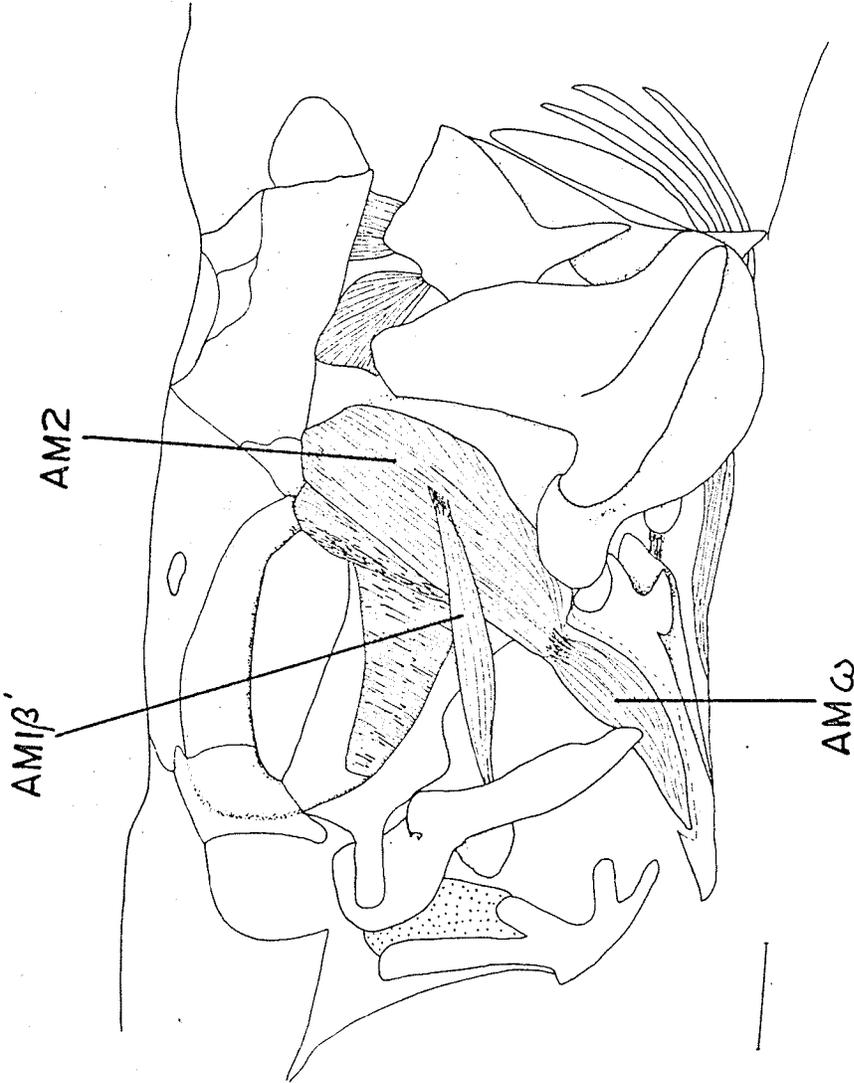
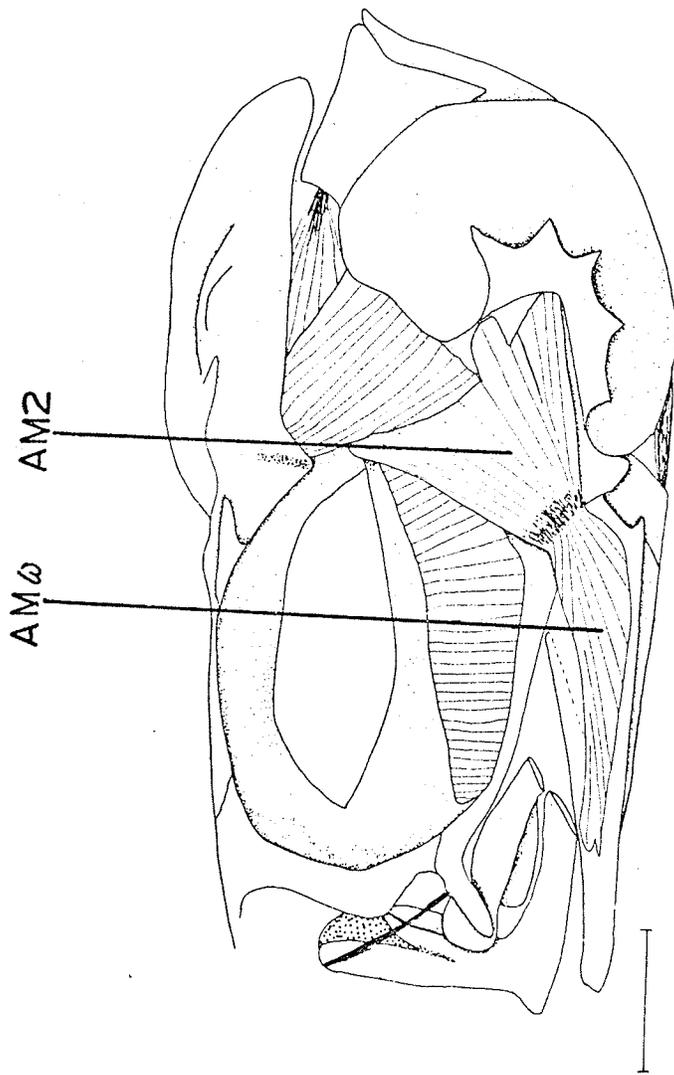


Figure 83. Lateral view of the deep cheek muscles  
of Trachyrincus helolepis, SOSC Reg. No. 309,  
98 mm HL.



rinchus innotabilis (figure 71), Coelorinchus japonicus (figure 72) and Macrourus berglax (figure 5), all of which have very large orbits. The  $A1\alpha$  section is invariably smaller than the  $A1\beta$ . The superficial cheek muscles of Trachyrinchus helolepis differ from those of other macrourids in being very long and thin, inserting directly on the maxilla, since the primordial ligament is absent, and being lateral to levator arcus palatini (figure 73).

Adductor mandibulae 2 originates on the metapterygoid, hyomandibula and preopercle and runs ventrally to the posterior edge of the mandible where it joins adductor mandibulae  $\omega$  through a short piece of connective tissue (figures 6, 82 and 83). A2 is parallel-fibered in all species examined (figures 6 and 75 to 83) except Macruronus novaezelandiae, where the fibers converge on an aponeuroses that runs the length of the muscle (figure 74).

#### B. Muscles Between the Cranium and Suspensorium

The levator arcus palatini originates on the cranium posterior to the orbit and runs diagonally posteroventrally to its insertion on the anterior edge of the preopercle. The adductor arcus palatini muscle courses from the parasphenoid to the endopterygoid. In Macruronus novaezelandiae (figure 74) and Steindachneria argentea (figure 75) it is small and located anteriorly in the orbit. In Bathygadus macrops it fills the posterior half of the floor of the orbit (figure 76) and in all others it extends for the entire

length of the orbit.

#### C. Muscles Between the Cranium and Opercle

The dilatator operculi originates on the cranium posterior to the levator arcus palatini and inserts on the anteromedial surface of the opercle anterior to its articulation with the hyomandibula (figures 5 and 55 to 73). In Trachyrincus helolepis it is oriented anteroposteriorly (figure 73), while in all others its course is diagonal.

Posterior to the dilatator operculi is the levator operculi, a small muscle that inserts on the medial surface of the dorsal side of the opercle posterior to the hyomandibular articulation ( figures 56,57,58,62,65,68,69). (Due to its small size and position medial to the opercle this muscle is not shown in all illustrations).

#### D. Ventral Muscles of the Head

There is a small intermandibularis muscle between the dentaries anteriorly in Bathygadus macrops (figure 84) and Trachyrincus helolepis (figure 94).

The geniohyoideus muscle is attached anteriorly to the medial surface of the dentaries and posteriorly to the hyoid and two of the branchiostegal rays. Between the dentaries the paired geniohyoideus muscles meet each other medially at a place where there is an aponeurosis that divides the anterior and posterior sections of the muscle, which are innervated by different nerves and contract at different times in the cycle of opening the mouth (Osse, 1969).

The large sternohyoideus muscle extends from the hyoid symphysis posteriorly to the anterior surface of the cleithrum (figures 84 to 94). Except as they vary in length with the length of the mandible and hyoid, there is very little difference between these muscles in the species examined.

There is a thin layer of hypaxial muscle ventral to the sternohyoideus, as well as hypaxial muscles that insert on the posterior surface of the cleithrum.

#### E. Epaxial Muscles

On the posterodorsal surface of the cranium there are muscles that extend posteriorly to join the dorsal muscles of the body, or epaxial muscles. The amount of area of the cranium over which these muscles insert varies within the family. Those with higher supraoccipital crests have more muscle attachment than the others. There is only a small amount of muscle attachment on the dorsal surface of the cranium in Abyssicola macrochir, Coelorinchus species and Trachyrincus helolepis.

#### X. Ligaments

##### A. Intrinsic Ligaments of the Jaws

There is a broad ligament from the lateral surface of the rostral cartilage to the medial surface of the head of the maxilla (figure 97).

The primordial ligament has been described in the description of muscles to the maxilla. It is diffuse in Macruronus novaezelandiae, Steindachneria argentea and

Figure 84. Ventral view of the cranial muscles of  
Bathygadus macrops, UMML 15193, 68 mm HL.

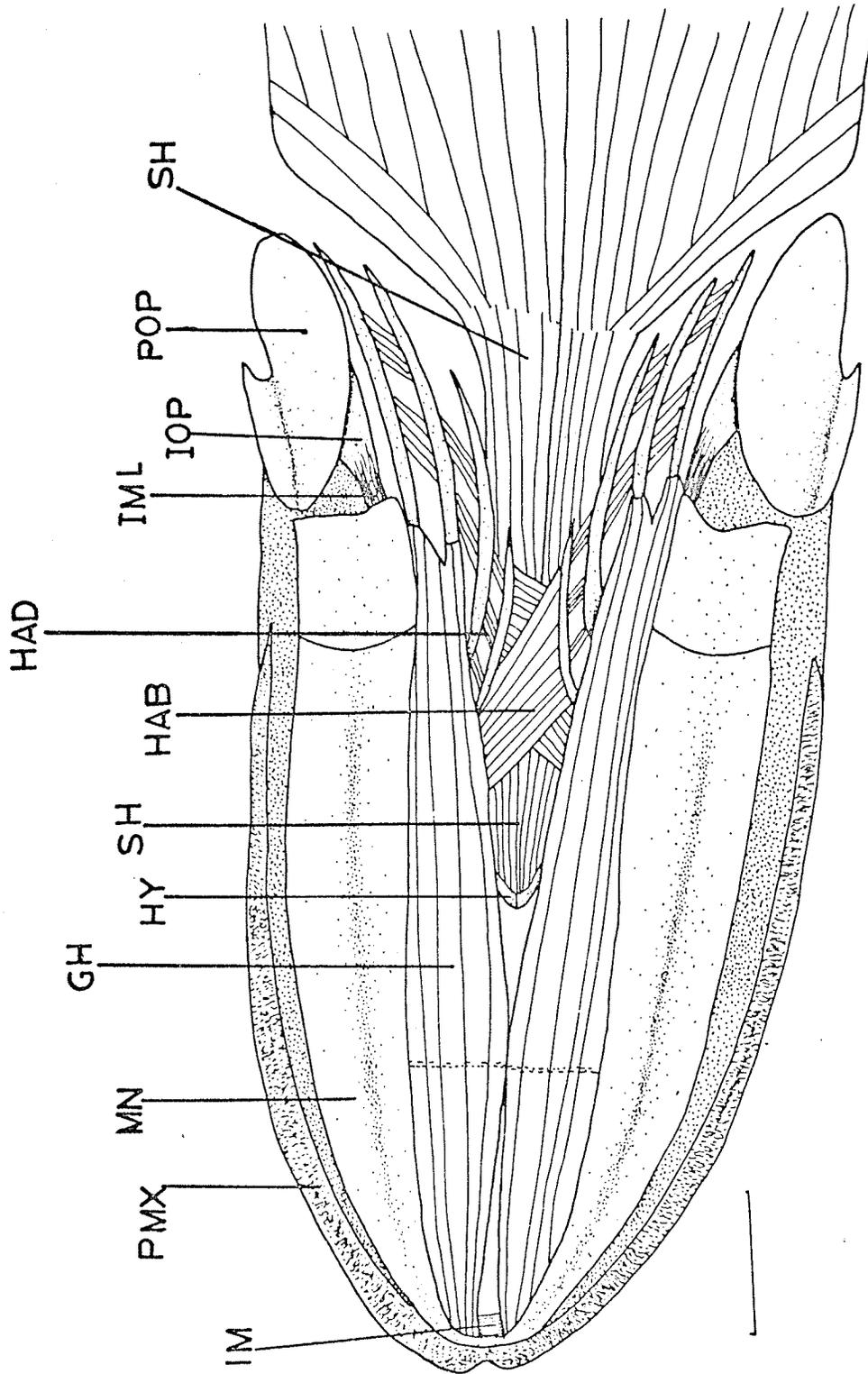


Figure 85. Ventral view of the cranial muscles of Malacocephalus occidentalis, UMML 25600, 51 mm HL.

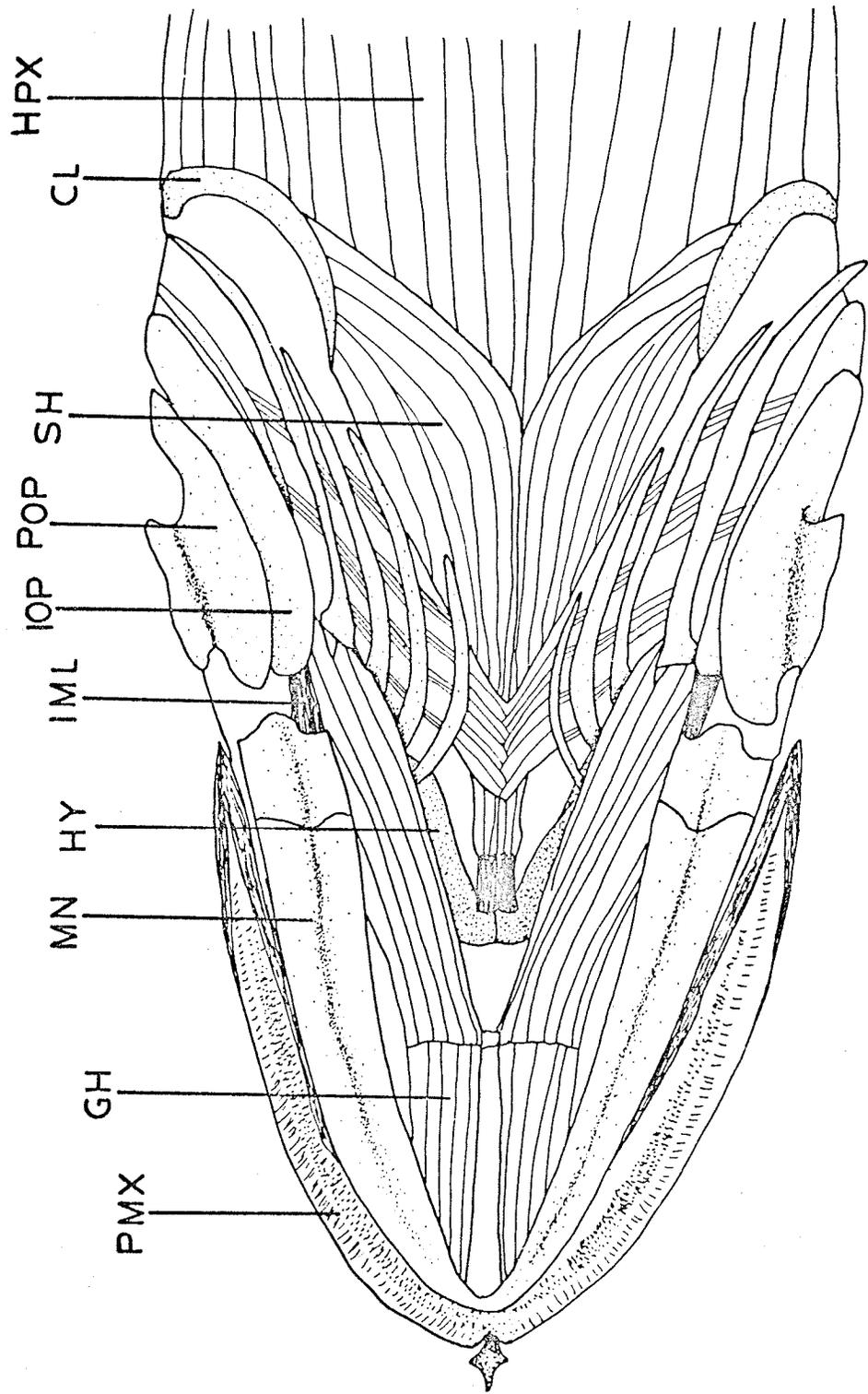


Figure 86. Ventral view of the cranial muscles of  
Nezunia bairdii, MCZ 51176, 65 mm HL.

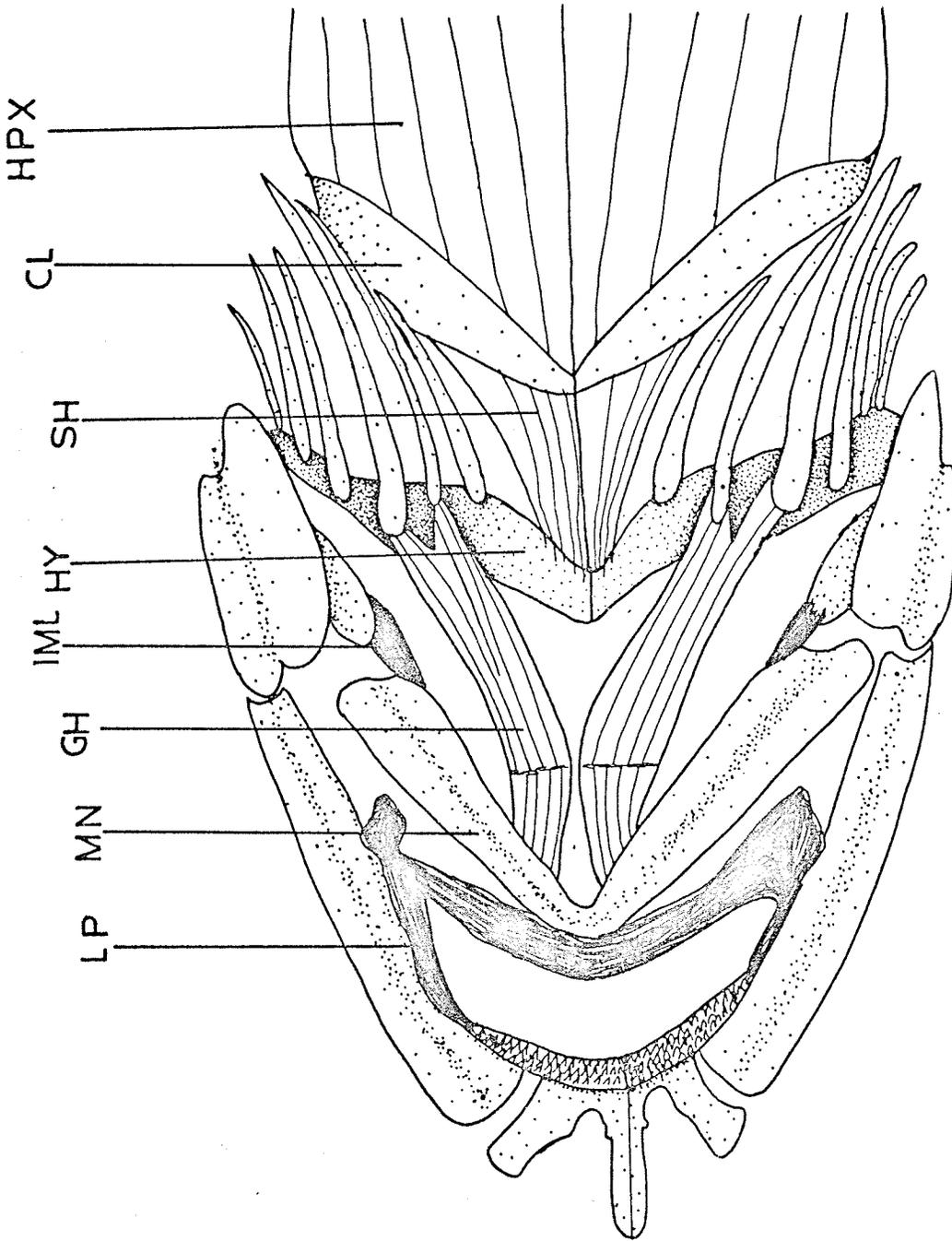


Figure 87. Ventral view of the cranial muscles of  
Mataeocephalus acipenserinus, USNM 55259, 42 mm HL.



Figure 88. Ventral view of the cranial muscles of  
Coryphaenoides rupestris, VIMS 00899, 82 mm HL.

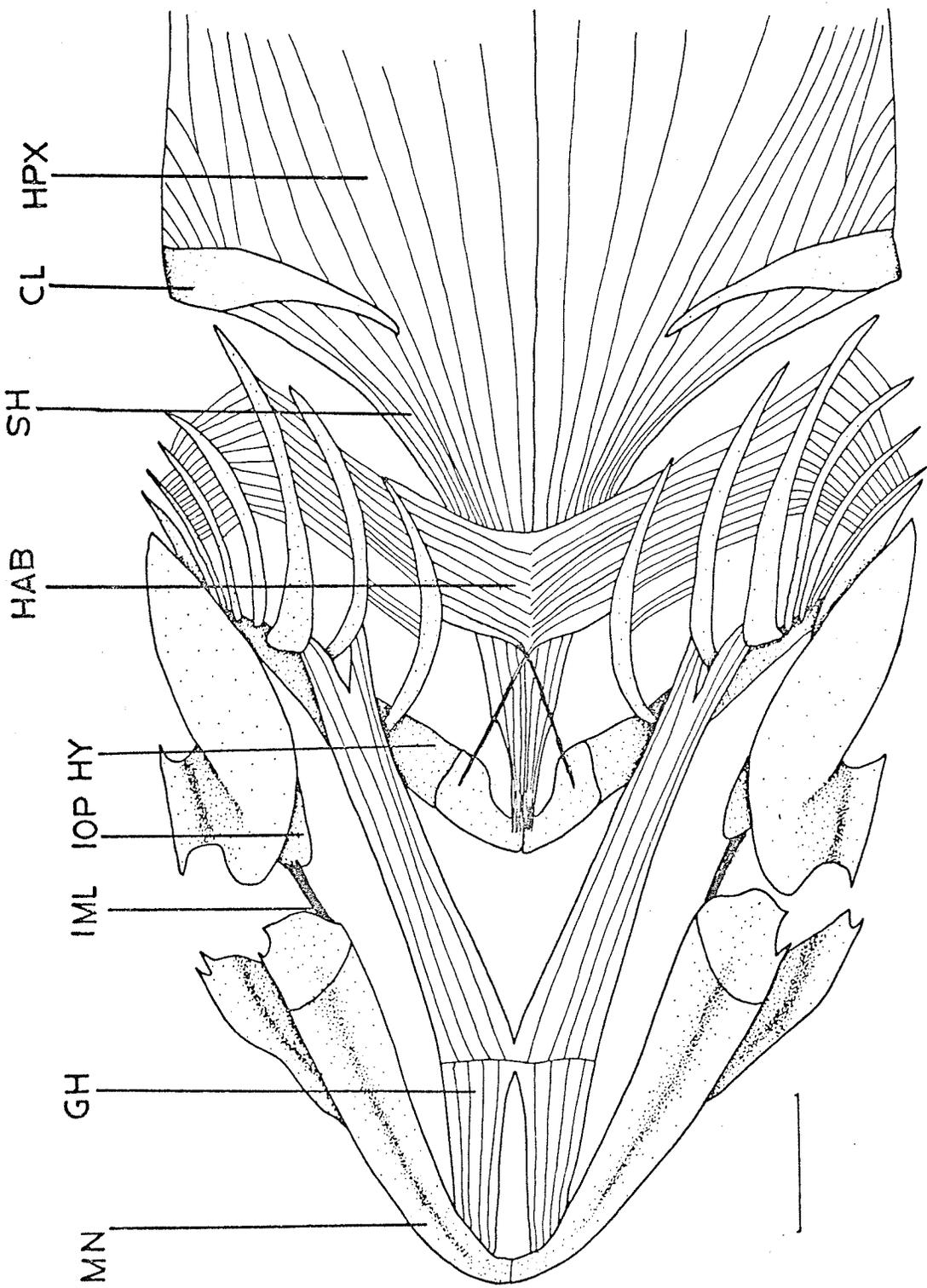


Figure 89. Ventral view of the cranial muscles of  
Coryphaenoides armatus, MCZ 51868, 78 mm HL.

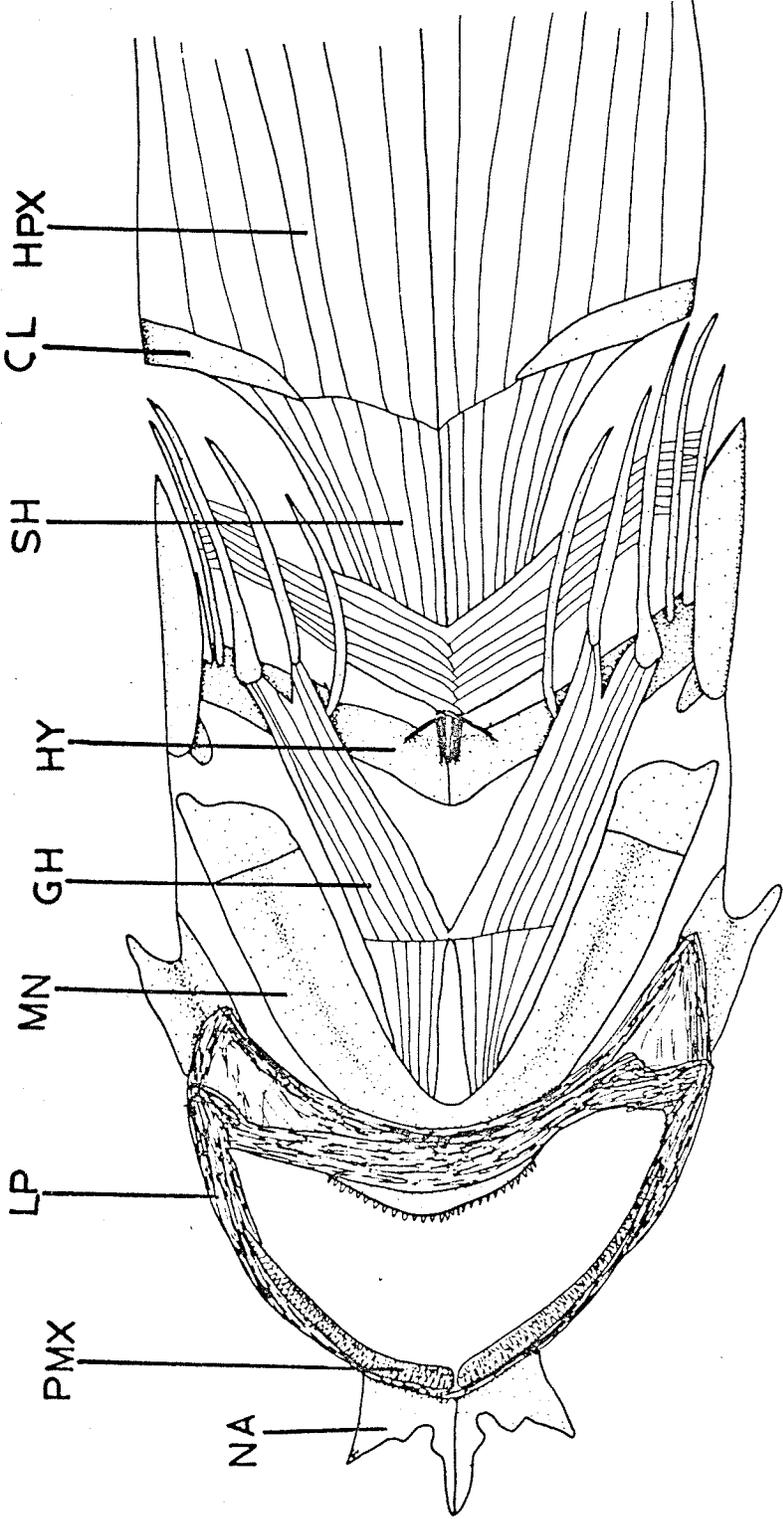


Figure 90. Ventral view of the cranial muscles of  
Coryphaenoides acrolepis, MCZ 51931, 156 mm HL.

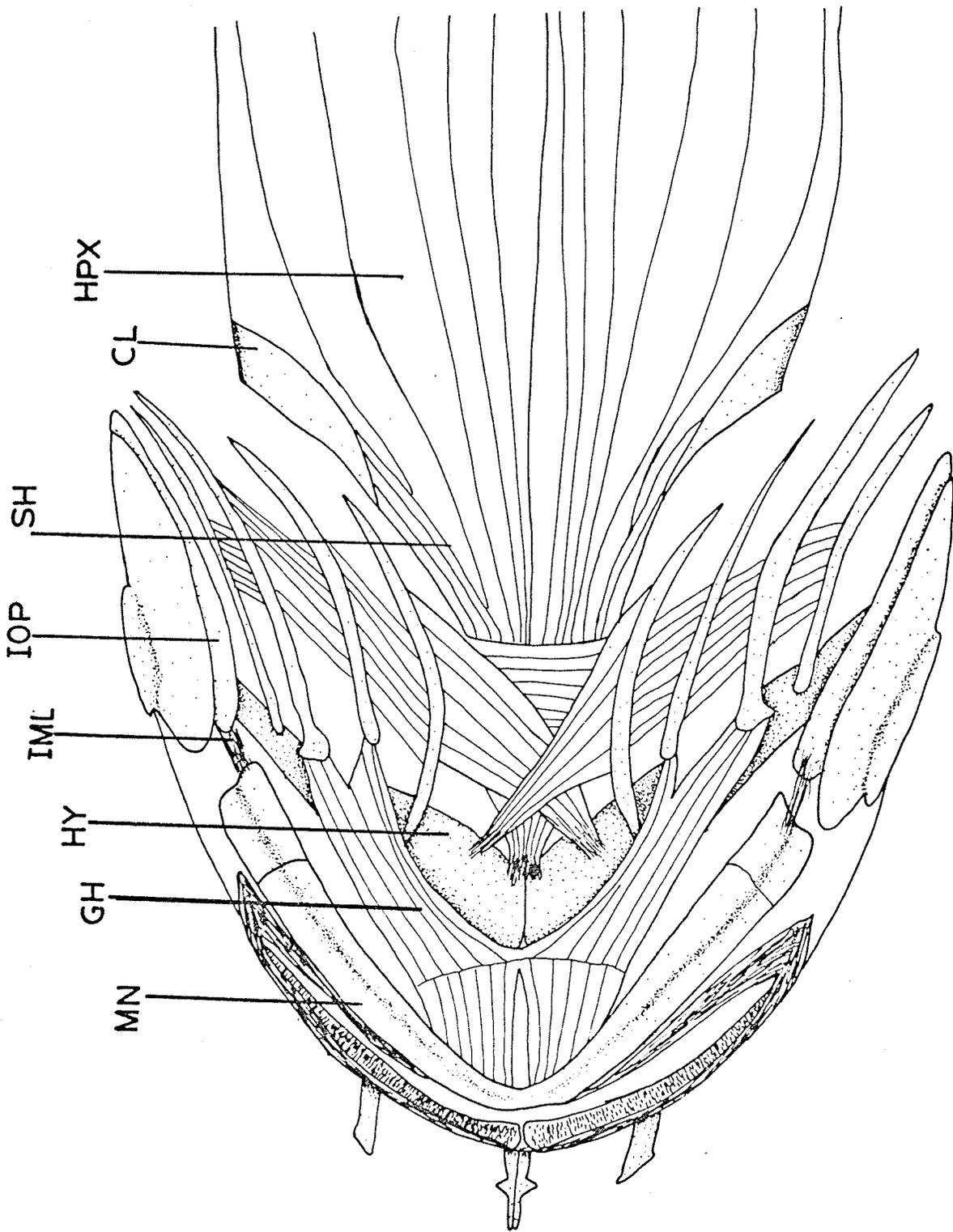


Figure 91. Ventral view of the cranial muscles of  
Coryphaenoides leptolepis, 51155, 78 mm HL.

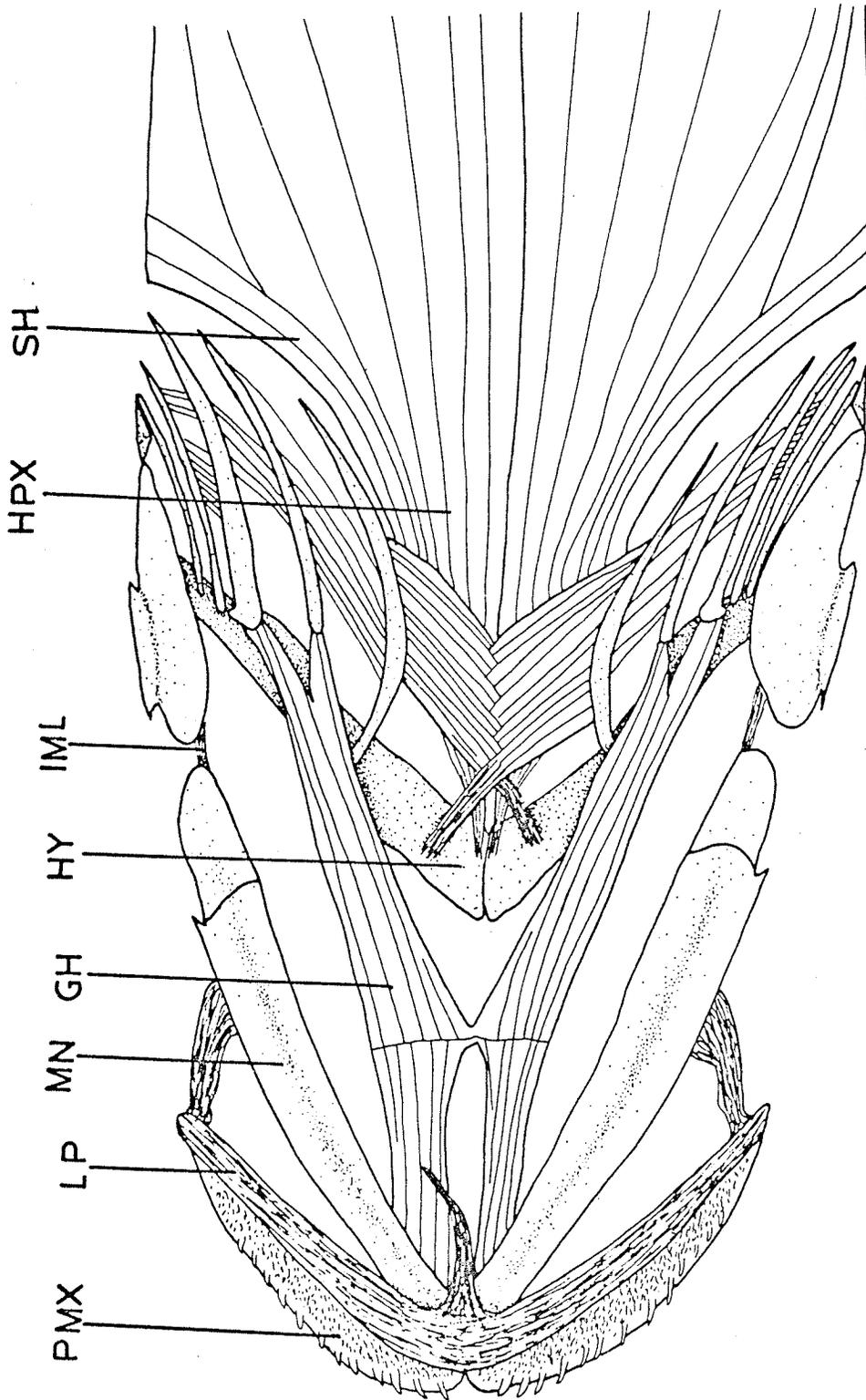


Figure 92. Ventral view of the cranial muscles of  
Coelorinchus occa, UMML 26794, 133 mm HL.

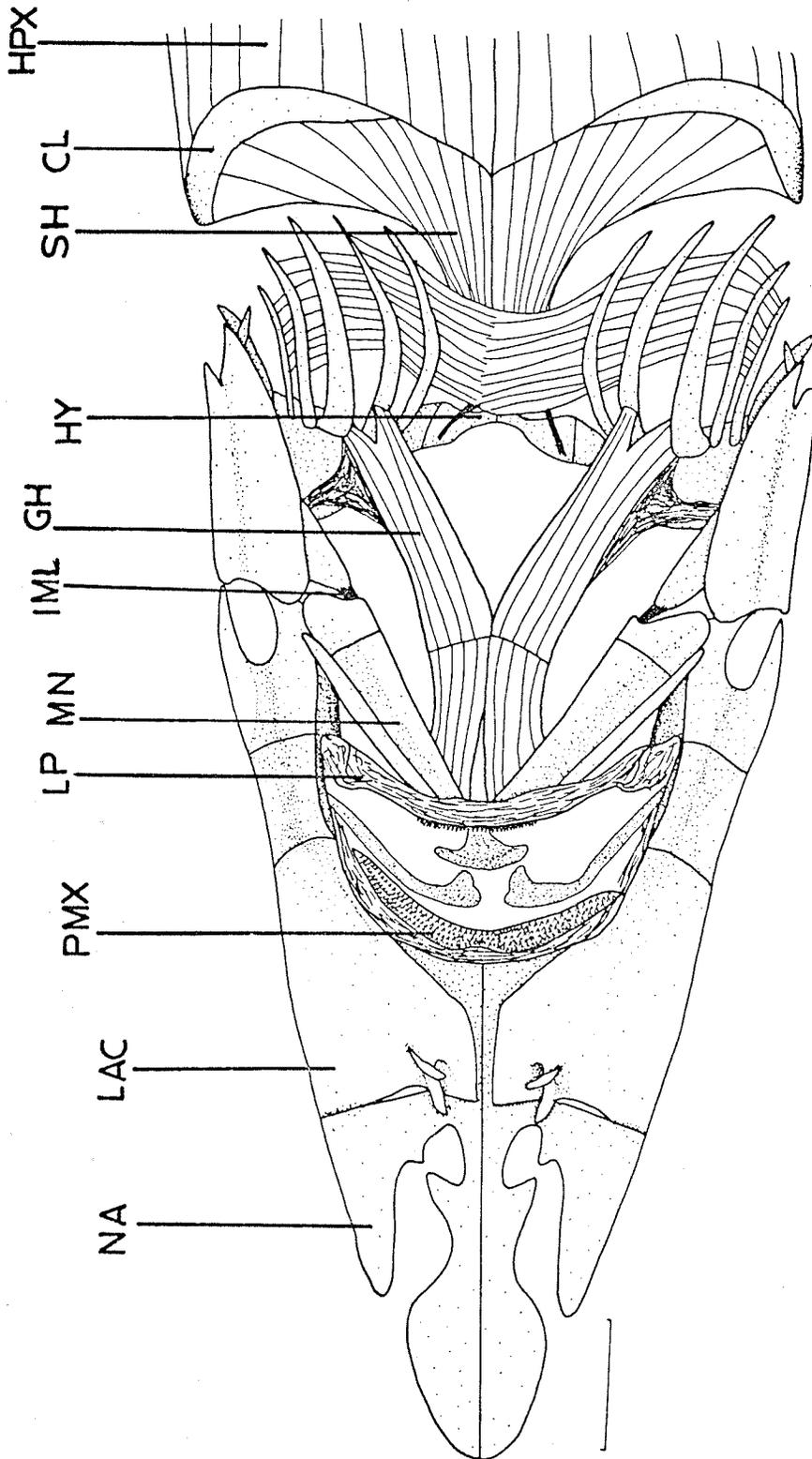


Figure 93. Ventral view of the cranial muscles of  
Coelorinchus innotabilis, LACM Elatanin 1718, 54 mm HL.

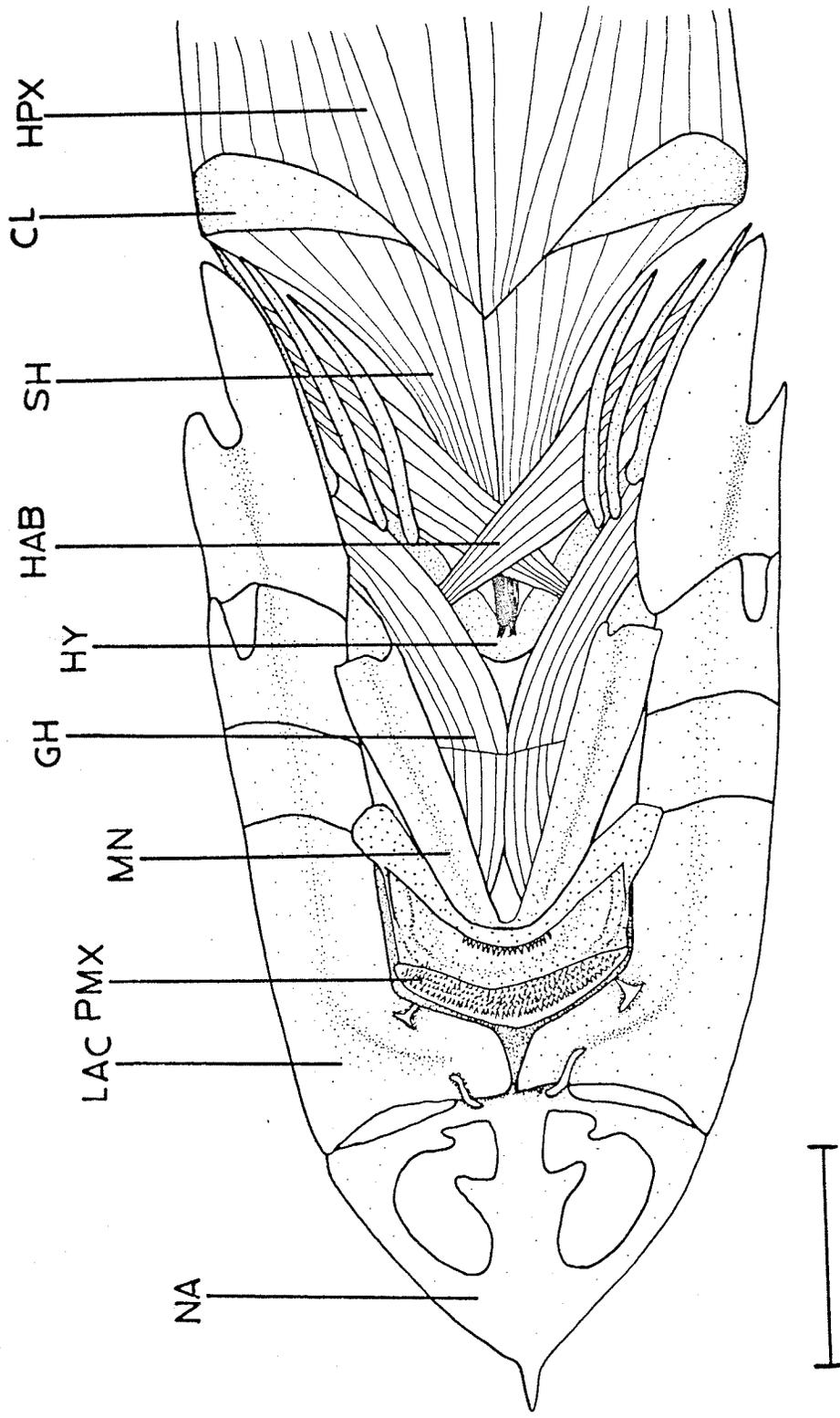
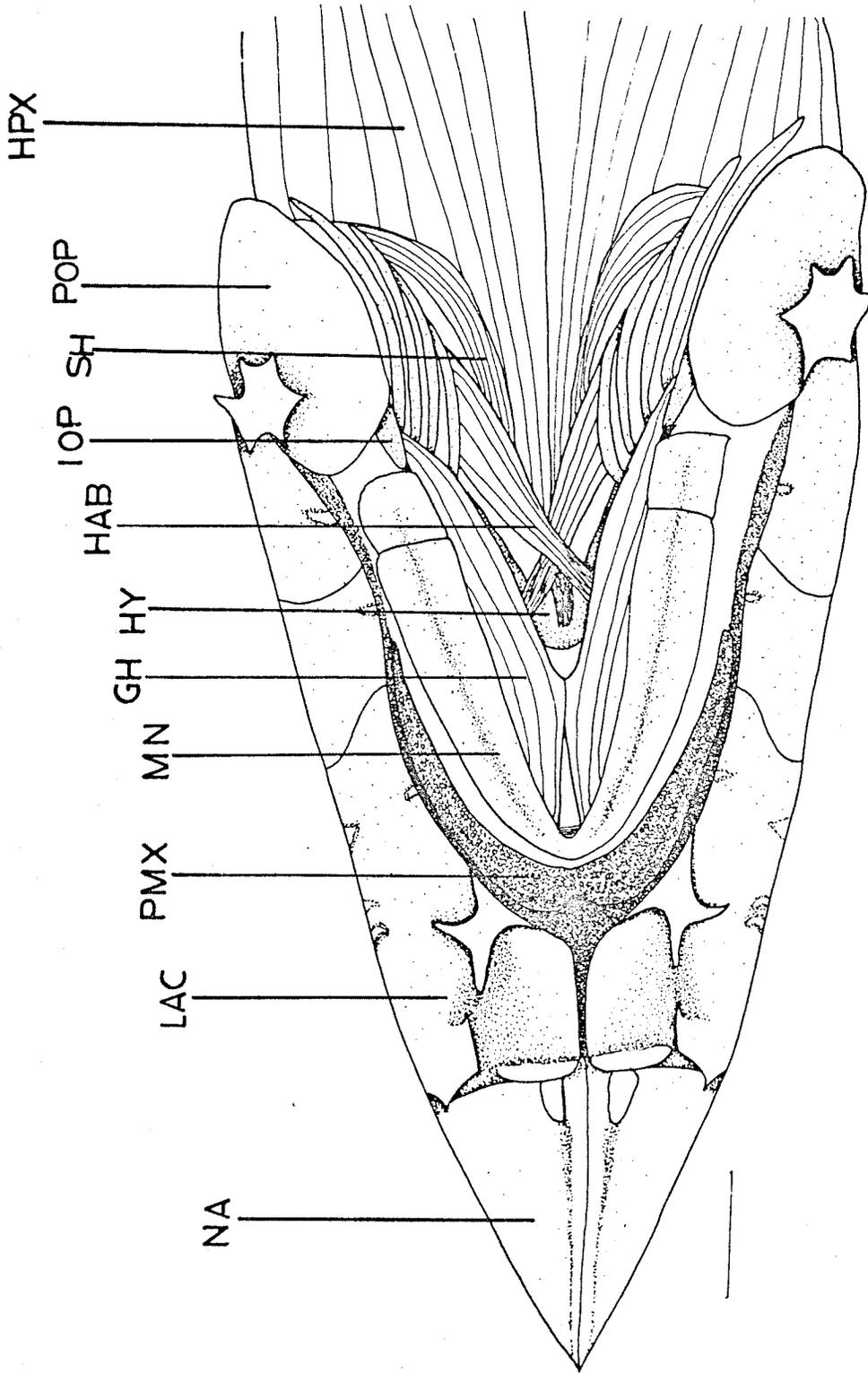


Figure 94. Ventral view of the cranial muscles of  
Trachyrincus helolepis, SOSC Reg. No. 309, 98 mm HL.



Bathygadus macrops, and is consolidated and strong in the macrourines. There is no primordial ligament in Trachyrincus helolepis.

The maxillo-mandibular ligament is a short, stout ligament from the medial surface of the posteroventral end of the maxilla to the lateral surface of the ascending process of the mandible.

There is some loose connective tissue between the alveolar process of the premaxilla and the maxillary ramus in all species examined. In Mataeocephalus acipenserinus, Macrourus berglax, Abyssicola macrochir and Coelorinchus species it is differentiated into a ligament from the post-maxillary process of the premaxilla to the distal end of the maxilla (figures 5, 67 to 72, 97).

The lip is an external ligament that connects the distal end of the alveolar process, the distal end of the maxilla and the anterior surface of the dentaries.

#### B. Other Ligaments of the Head

There are strong crossed ligaments from the upper jaw anteriorly to the cranium and suspensorium. The premaxillary-palatine ligament extends from the distal end of the ascending processes of the premaxilla posteriorly to the base of the maxillary process of the palatine. The ethmo-maxillary ligament extends from the lateral surface of the head of the maxilla to the anterior surface of the ethmoid.

The interoperculo-mandibular ligament runs between the

posteroventral corner of the mandible to the anterior edge of the interopercle.

The hyoid-interopercular ligament is short and wide, connecting the medial surface of the interopercle with the lateral surface of the hyoid.

In many macrourids there is a ligament from the horizontal surface of the lacrimal, posterior to the lacrimal spine, to the palatine ventral to its articulation with the prefrontal.

## COMPARATIVE FUNCTIONAL MORPHOLOGY

The greatest osteological variation within the macrourids is found in the size and shape of the nasal bones, infraorbital series and preopercle. There are large differences within the family in the morphology of the premaxilla and the length of the mandible, and thus in the protrusibility of the premaxilla and the size of the mouth when fully opened. Small differences in the suspensorium and hyoid are important in the degree of lateral expansion of the oral cavity.

## I. Rostrum Architecture

The rostrum is the part of the head anterior and dorsal to the mouth. In macrourids the skeletal support for the rostrum is the nasals, which are held firmly to the cranium. The long rostrum of the macrourids is the most striking feature of the shape of the head, and an understanding of its form will lead to an understanding of the function of this unusual anatomical feature found only in this and a few other groups of teleosts.

The most generalized species, Macruronus novaezelandiae, Steindachneria argentea and Bathygadus macrops have no rostrum, the nasals being small and separate from each other distally. The nasals of Bathygadus macrops have two distinct anterior corners, similar to the medial and lateral processes of more specialized species.

There is a short rostrum in Lepidorhynchus denticulatus, Malacocephalus occidentalis, Coryphaenoides leptolepis and Coryphaenoides pectoralis, where the nasals are united along the midline. The scales are uniform in size over the heads of these species, and there is no contact between the lacri-mal and nasals.

Moderately long rostrums occur in Nezumia bairdii, Coryphaenoides rupestris, Coryphaenoides carapinus, Coryphaenoides armatus, Coryphaenoides acrolepis, Macrourus berglax, Coelorinchus coelorinchus carminatus, Coelorinchus chilensis, Coelorinchus jordani. The rostrum is very long in Mataeocephalus acipenserinus, Abyssicola macrochir, Trachyrincus helolepis and the other species of Coelorinchus. The proportions of rostrum length, head size and shape of the body are similar in Mataeocephalus, some species of Coelorinchus and Trachyrincus, but there are marked differences between them in the shape of the nasals, the scales of the head and ridges of the head.

There are modified scales on the three anterior tips of the rostrum in Nezumia bairdii, Coryphaenoides armatus and Coryphaenoides acrolepis. Coryphaenoides carapinus has longer nasals than these three species and the rostrum bears no modified scales. Coryphaenoides rupestris has a high, round rostrum covered uniformly with small scales and supported by nasals with narrow anterior processes.

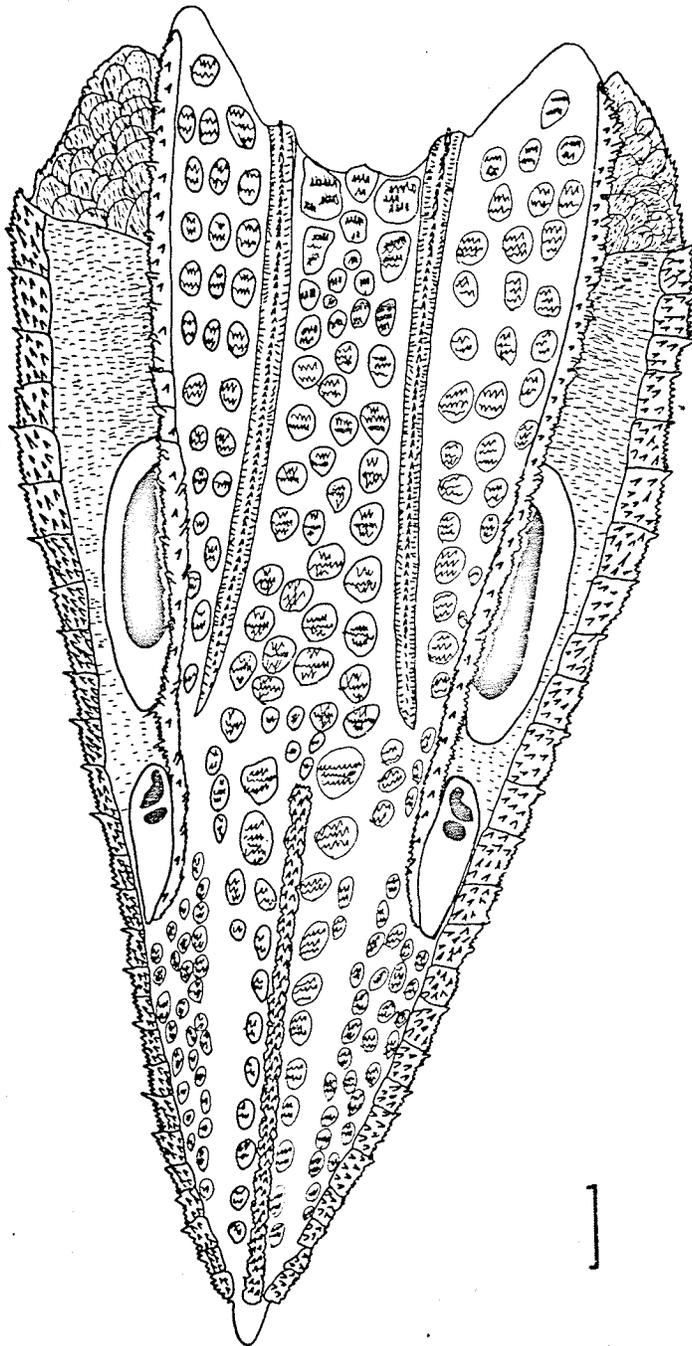
Mataeocephalus acipenserinus has closely imbricated

scales along the lateral margins of the rostrum and on the strong infraorbital ridge, and cap-like scutes on the distal ends of the medial processes of the nasals. The nasals are long and have long, narrow medial processes. There is a cushion of tough connective tissues between the lateral and medial processes.

In Macrourus berglax, Abyssicola macrochir and all species of Coelorinchus, the infraorbital series forms a ridge that is continuous anteriorly with the lateral edge of the rostrum and posteriorly with the preopercular shelf. In addition, there are strong external ridges on the dorsal surface of the head where small scales are held firmly to the bone in a series along a crest of bone. Several ridges are enumerated by Okamura (1970b, p.67). One median and two pairs of ridges are prominent in Coelorinchus occa (figure 95). They run along the dorsal keel of the nasals and frontals, the lateral edge of the cranium dorsal to the orbit, and from the anterior end of the frontals to the parietal-epiotic crest (lambdoidal crest).

It has been suggested previously that the rostrum may be used as a shovel in bottom sediments (Marshall and Bourne, 1964). The ridges of the head serve as trajectories for the forces created as the fish pushes and overturns sediment. The major trajectory is that of the lateral margin of the nasals, lacrimal, first two infraorbitals and preopercular shelf. This ridge is further strengthened in three species, Coelorinchus

Figure 95. Dorsal view of the head of Coelorinchus  
occa, UML 26794, 133 mm HL.



jordani, Coelorinchus innotabilis and Coelorinchus japonicus, where the medial and lateral processes of the nasals are united along the lateral margin. The dorsal ridges serve as additional trajectories - the medial ridge along the nasal and frontal crest takes up some of the force anteriorly, while the four posterior ridges disperse the force from the posterior of the nasals to the neurocranium, which is the most solid part of the head.

The head and rostrum of Trachyrincus helolepis are more dorsoventrally depressed than in Coelorinchus. The nasals are different in being of much thinner bone and occupying more space than those with rostrums of comparable length. The lacrimal is widest anteriorly, where it forms a broad horizontal shelf ventral to the posteroventral margin of the nasal. The infraorbital series, though narrower than in Coelorinchus, is in contact with the preopercle through a process of the third infraorbital. The scales of the head and body are uniform, forming no external ridges. The close imbrication of the heavily keeled scales makes the skin rigid, so that the entire dorsal surface of the head is a widening trajectory for forces generated when the rostrum is used for digging.

The long rostrums of Mataeocephalus, Coelorinchus and Trachyrincus are similar in overall shape but different from each other in the shape of the nasals, the arrangement of the lacrimal, infraorbitals and preopercle, and the scales of the head. The rostrum of Mataeocephalus has only a strong medial

process of the nasals and some enlarged scales, while the nasals of Coelorinchus are markedly stronger and the dorsal ridges of the head distribute force to the neurocranium. The strength of the rostrum of Trachyrincus depends on scales and the support of the lacrimal.

## II. Protrusibility of the Upper Jaw

Protrusibility of the upper jaw is the motion of the ascending processes of the premaxillae out of a socket in the cranium (Eaton, 1935; Schaeffer and Rosen, 1961). Non-protrusible jaws differ in that the alveolar process of the premaxilla swings anteroventrally with the maxilla while the upper end remains in place in the cranium. Protrusible mouths occur in several groups of teleosts and have evolved in several independent lines (Alexander, 1966, 1967a; Liem, 1967, 1970). Protrusibility does not occur in the other families of the order Gadiformes, to which the Macrouridae belongs.

The jaws of three species examined here, Macruronus novaezelandiae, Steindachneria argentea and Bathygadus macrops, are non-protrusible and resemble in that way the jaws of Gadus (Tchernavin, 1953; Schaeffer and Rosen, 1961) and Merluccius (Joppien, 1972). The ascending process of the premaxilla is short and the premaxilla swings with the maxilla as the mouth opens to make a circular opening (Rosen and Patterson, 1969).

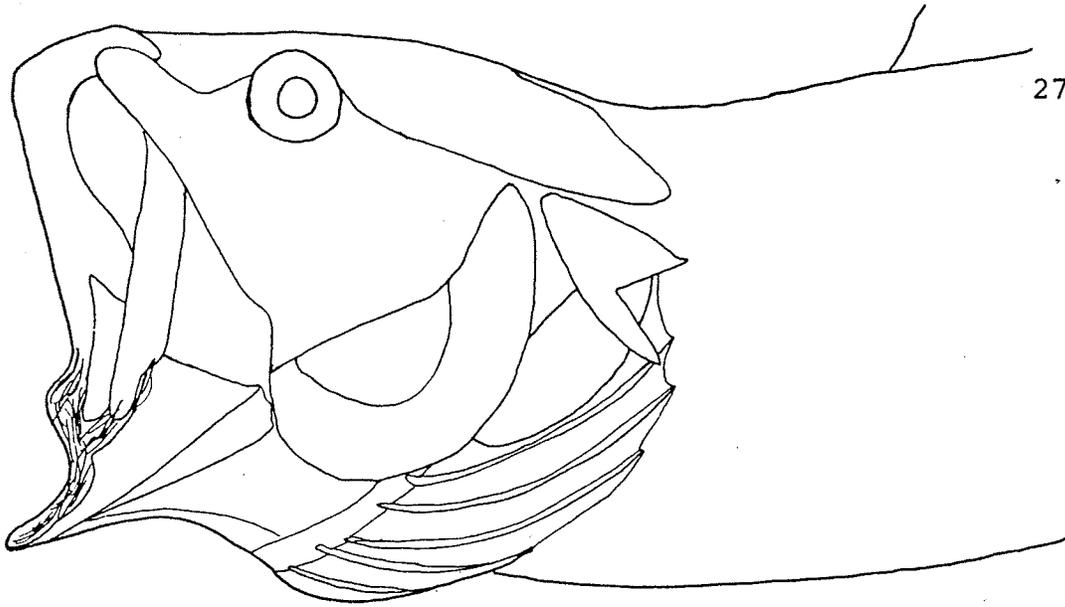
The length of the ascending processes of the premaxilla determine the degree of protrusibility, since it is the sliding of these processes that is involved in protrusibility. Okamura (1970b) has used this observation to create an index of protrusibility, the ratio of the length of the ascending process to the length of the alveolar process. This is not a good quantitative index of the relative amount of protrusibility in different species, that is, of the length of the ascending process corrected for the size of the fish, since there is a positive correlation between longer ascending processes and shorter alveolar processes. If one wanted to quantify protrusibility in such a way, it would be better to use as a measurement for standardization something like the postrostral length of the head, which does not vary directly with the length of the ascending process. No such attempt was made here because of the limited number of species available.

In the macrourine rattails and Trachyrincus the ascending processes of the premaxillae and the rostral cartilage slide anteroventrally relative to the cranium as the mouth opens. This results in the fully open mouth being oriented anteroventrally. In those species with very long ascending processes and a short mandible the fully open mouth is a short tube.

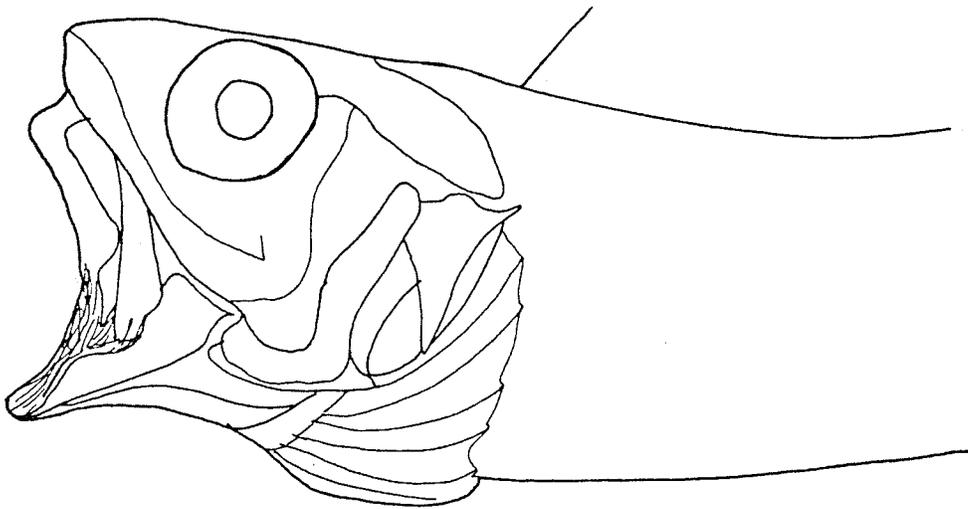
There is a correlation between shorter mandibles and longer ascending processes in most of the species examined. Those with non-protrusible premaxillae have large mouths that open to a very large anterior gape (figure 96A), while those

Figure 96. Lateral views of preserved specimens with mouths fully open. A. Bathygadus macrops  
B. Malacocephalus occidentalis C. Coelorinchus occa.

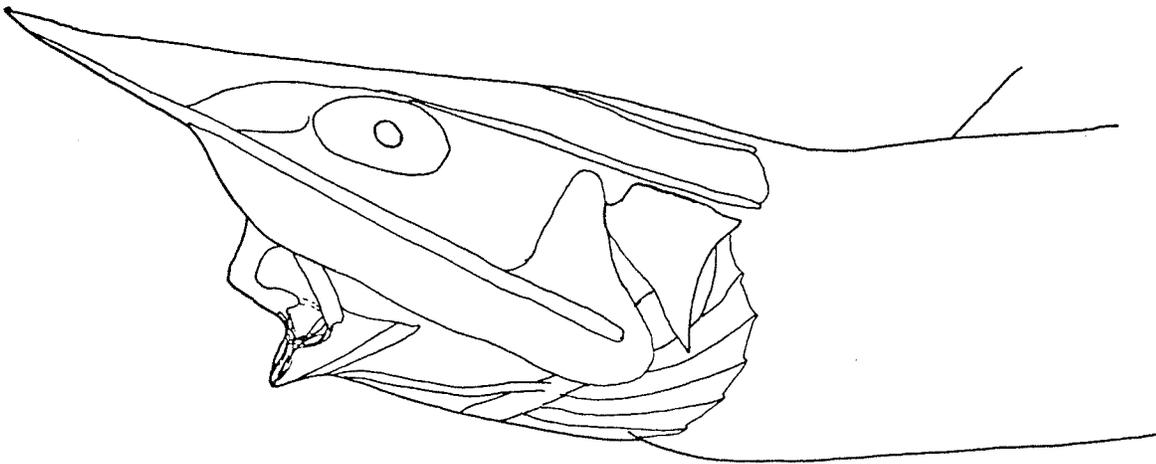
A



B



C

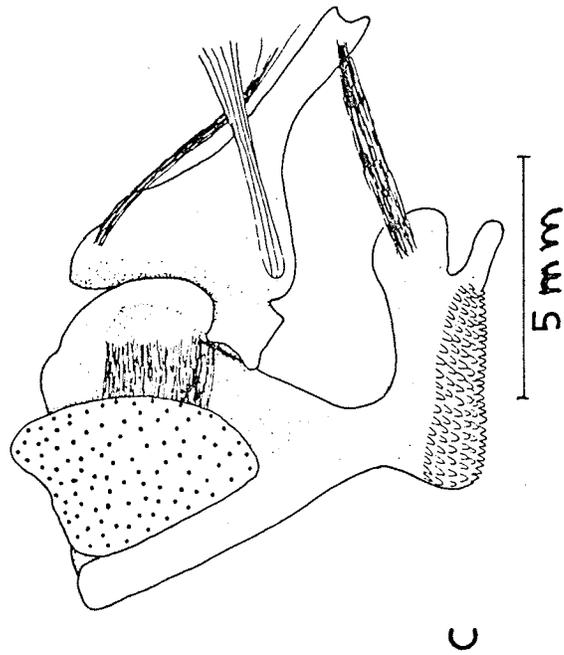
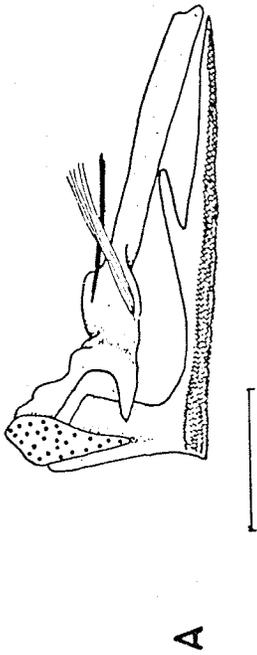
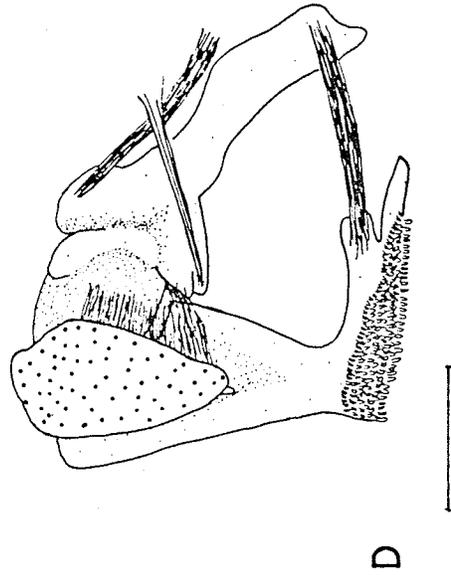
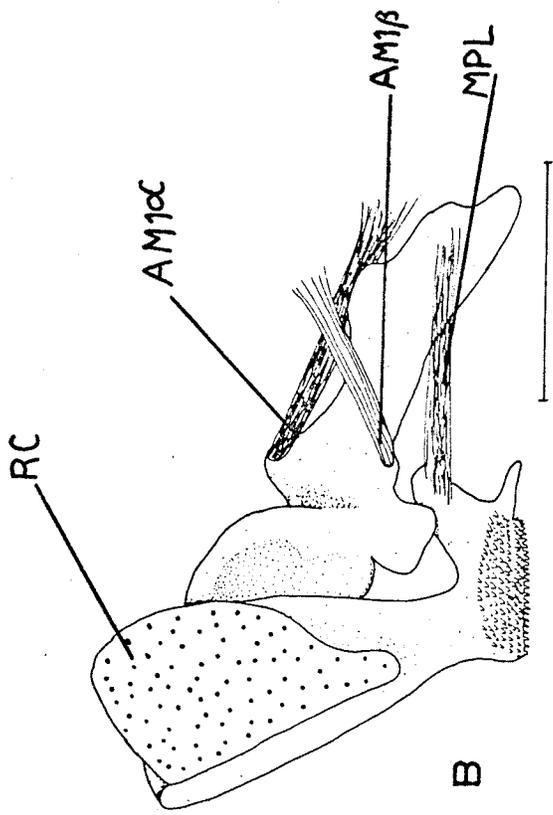


with small, protrusible mouths open to a much smaller width (figure 96C), and many are intermediate between these extremes (figure 96B).

In macrourids with highly protrusible small mouths, the head of the maxilla is much wider than in those with smaller, less protrusible mouths. The maxilla is widest just posterior to the palatine articulation, and the insertion points of adductor mandibulae 1  $\alpha$  and adductor mandibulae 1  $\beta$  on the maxilla are farthest from each other in those with highly protrusible premaxillae. Figure 97 shows the premaxilla and maxilla and associated ligaments of Trachyrincus helolepis, Mataeocephalus acipenserinus, Coelorinchus innotabilis and Coelorinchus occa. Trachyrincus shows the condition typical of the macrourids with slightly protrusible upper jaws, with the two divisions of the adductor mandibulae inserting near each other, while Coelorinchus occa shows the opposite extreme with adductor mandibulae 1  $\beta$  inserting anteriorly on the premaxillary condyle and the primordial ligament inserting on the high dorsal process of the maxilla.

An analogous situation has been described in the carp, where the two muscles inserting on the maxilla have widely separated points of insertion (Ballintijn, van den Burg and Egberink, 1972). Electromyographic recordings have shown that the more ventral muscle, which inserts more dorsally on the maxilla, is active during the opening of the mouth, and that its contraction is important in determining the angle at which

Figure 97. Medial view of the maxilla, premaxilla and rostral cartilage. A. Trachyrincus helolepis  
B. Mataeocephalus acipenserinus C. Coelorinchus innotabilis  
D. Coelorinchus occa.

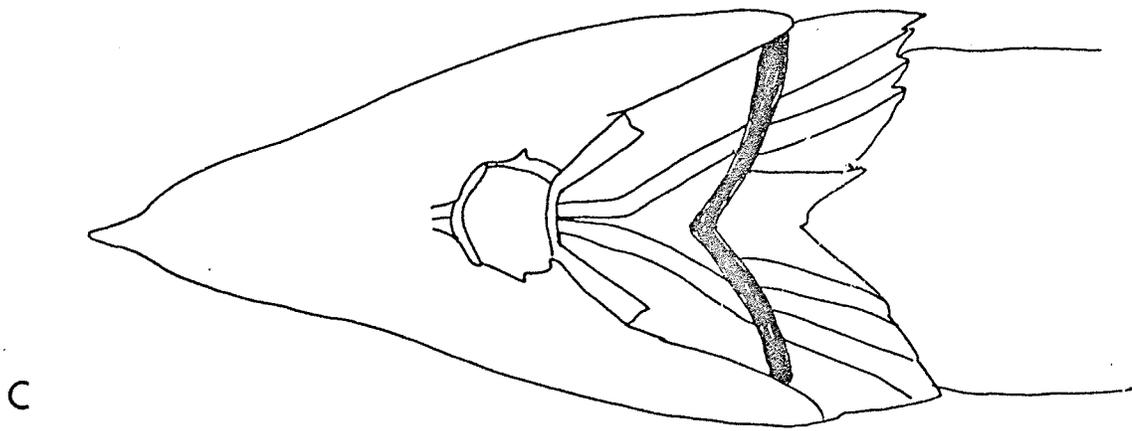
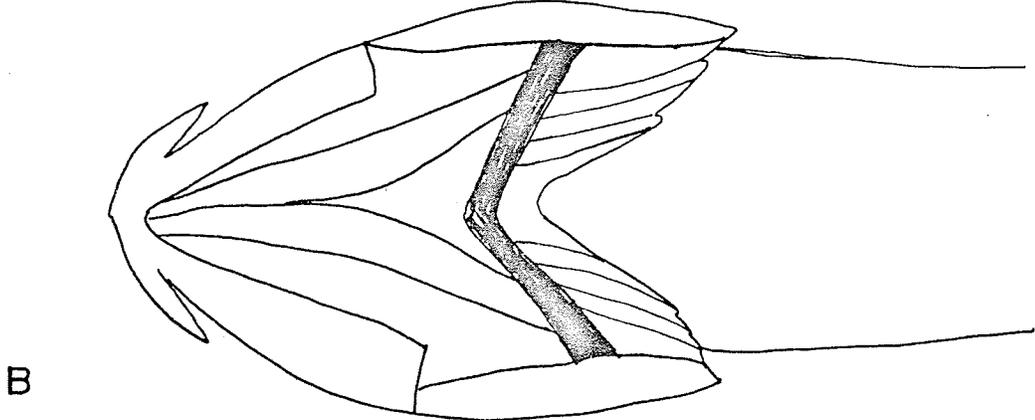
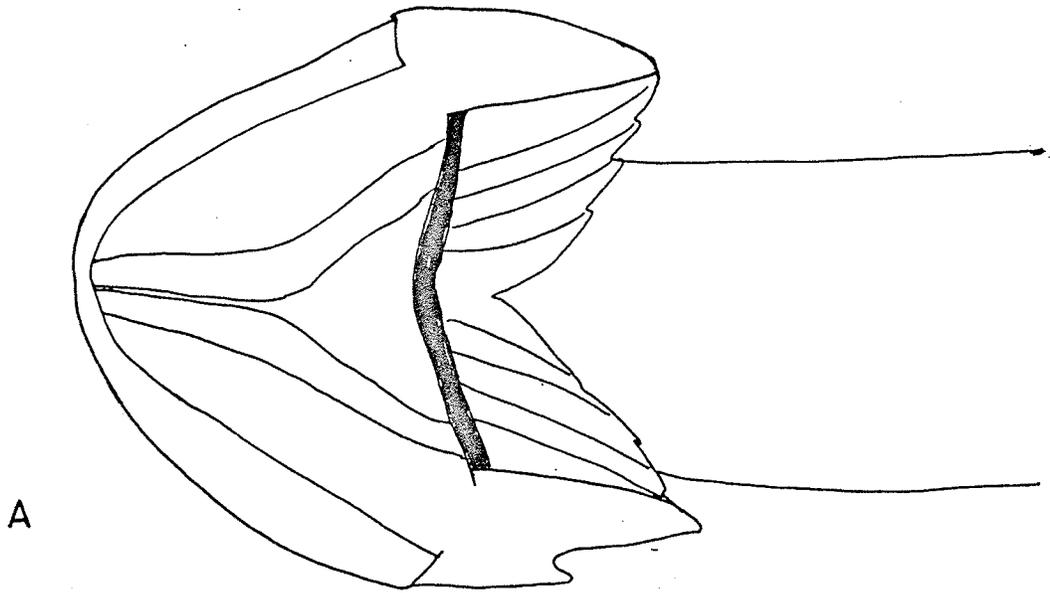


the premaxilla is protruded. Pulling on the primordial ligament in fresh macrourid specimens resulted in the protrusion of the premaxilla (figure 11). This evidence, and the analogy with the carp, suggest that the contraction of adductor mandibulae 1  $\alpha$  is important in the protrusion of the premaxilla, and its insertion high on the maxilla, as occurs in species with highly protrusible upper jaws, is important in this function.

### III. Suspensorium and Hyoid

In the specialized macrourids with highly protrusible mouths the suspensorium and hyoid bars are shorter than in the more generalized forms. The result of this in the functioning of the head is a difference in the amount of lateral expansion of the oral cavity when the mouth is opened to its fullest extent (figure 98). In Bathygadus macrops with mouth fully open and the orobranchial cavity expanded to its full extent, the gill filaments are exposed and the hyoid bars have almost no angle between them in ventral view. An intermediate situation occurs in Malacocephalus occidentalis, where the gill covers are not flared quite so far and there is a small angle between the hyoid bars. The third step in this progression is shown by Coelorrinchus occa, where there is a small angle between the hyoid bars and the orobranchial cavity is not expanded widely. The head of Coelorrinchus occa is dominated by the large nasals

Figure 98. Ventral views of preserved specimens with the mouths fully open. A. Bathygadus macrops B. Malacocephalus occidentalis C. Coelorinchus occa. Hyoid is shown in black.



and infraorbitals, so that the lateral expansion of the orobranchial cavity seems to make little difference in the appearance of the head.

#### IV. Summary

There are great differences within the Macrouridae in the architecture of the rostrum, in the size and degree of protrusibility of the jaws, and in the amount of maximum lateral expansion of the orobranchial cavity. Coelorinchus species are characterized by having long rostrums strengthened by external ridges, small highly protrusible mouths, and little lateral expansion of the mouth. These extreme morphological characteristics function together to enable Coelorinchus to utilize certain food resources. The functional significance of this specialized head morphology can best be understood through the study of stomach contents, since direct observations of feeding are presently impossible.

## FEEDING HABITS OF THE MACROURIDAE

One direct means of determining the feeding habits of fishes is to open the stomach and intestine and examine the food that was ingested just prior to capture. There are some prejudices inherent in the analysis of stomach contents. Notably, the soft prey organisms are digested more rapidly than those with hard skeletons, teeth or shells, so that the proportion of prey organisms found in the stomachs may not be an accurate reflection of the proportion ingested.

The stomach contents of the study material were examined. They are summarized, together with the results of several studies of macrourid stomach contents and observations in systematics studies in Table 1.

The food items found are for the most part whole animals that can be divided into three categories on the basis of habitat. Fishes, cephalopods and euphausiids are active swimmers, and if they are eaten alive, the predator probably swims after them. The second category of prey consists of several types of crustaceans, a few polychaetes, and some fishes that live in association with the sediment surface and spend at least part of their time swimming over the bottom. Those animals that dwell within the sediment or never leave the sediment surface, the echinoderms, gastropods, bivalves and most polychaetes, comprise the third category.

Table 1. Stomach contents of macrourids.

ref--reference      no.--number of specimens with contents  
 size--total length in centimeters of the largest specimen  
 \*--head length in millimeters      + length from snout to anal  
 fin in millimeters

fish--fish remains  
 cep--cephalopods  
 euph--euphausiids  
 cop--copepods  
 dec--decapod crustaceans  
 mys--mysids  
 amph--amphipods  
 per--other peracarid crustaceans (tanaids, cumaceans, isopods)  
 poly--polychaetes  
 ech--echinoderms, primarily ophiuroids  
 mol--molluscs other than cephalopods (bivalves and gastropods)

## Abbreviations for references

- HH Haedrich, R.L. and N. Henderson 1974. Pelagic food of *Coryphaenoides armatus*, a deep benthic rattail. *Deep-Sea Research* 21: 739-744.
- MB Maurer, R.O. and R.E. Bowman 1975. Food habits of marine fishes of the northwest Atlantic. Data Report. Northeast Fisheries Center, Laboratory Reference 75-3.
- MI Marshall, N.B. and T. Iwamoto 1974. Family Macrouridae in Fishes of the Western North Atlantic, vol. 6:496-665.
- OO Okamura, O. 1970. Studies of the macrouroid fishes of Japan. *Repts. Usa Biol.Sta.* 17: 1-179.
- PA Percy, W.G. and J. Ambler 1974. Food habits of deep sea macrourid fishes off the Oregon Coast. *Deep-Sea Research* 21:745-759.
- PG Geisdorfer, P. 1973. Regimes alimentaires de Macrouridae. *Bull. Mus. Natl. d'Hist. Natur.* 3 ser. 161: 285-295.
- PTP Pamela T. Polloni, unpublished data
- TM this study
- Nov. Novikov, N.P. 1970 cited in Percy and Ambler, 1974.
- Pod. Podrazhanskaya, S.G. 1967 cited in Percy and Ambler 1974.

Species ref no size fish cep euph cop dec mys amph per poly ech mol

Bathygadus macrops	TM	3	54	X														
Bathygadus antrodes	OO	3	55		X													
Gadomus arcuatus	TM	2	58		X				X									
Gadomus longifilis	MI	2	30					X										
Gadomus colletti	OO	12						X										
Lepidorhynchus denticulatus	TM	4	75*								X			X				X
Hymenocephalus italicus	TM	3	25		X				X									
Hymenocephalus striatissimus	OO	20	20		X				X									
Malacocephalus occidentalis	TM	2	29											X				
Malacocephalus occidentalis	MI	1	38						X									X
Malacocephalus laevis	MI							X										X

Species ref no size fish cep euph cop dec mys amph per poly ech mol

Malacocephalus laevis	OO	9	52		X	X													
Nezumia condylura	OO	8	21		X		X												X
Cetonurus globiceps	TM	3	27		X			X											X
Cetonurus globiceps	MI	1	45			X													
Trachonurus villosus	TM	3	45			X													X
Mataeocephalus acipenserinus	TM	4	18				X												X
Mataeocephalus tenuicauda	TM	2	27					X											X
Odontomacrus murrayi	MI	1	50						X										
Echinomacrus mollis	MI	2								X									X
Coryphaenoides rupestris	Pod.									X									
Coryphaenoides carapinus	PTP	30	20-49 <sup>+</sup>								X								X
		34	50-79 <sup>+</sup>								X								X
		20	80-124 <sup>+</sup>								X								X



Species	ref	no	size	fish	cep	euph	cop	dec	mys	amph	per	poly	ech	mol
Macrourus berglax	MI			X				X		X			X	X
Abyssicola macrochir	OO	14	22-68	X		X		X						
Coelorinchus coelorinchus	PG	3	31			X								
Coelorinchus coelorinchus carminatus	MB	14	73*			X		X	X			X		
Coelorinchus coelorinchus carminatus	TM	3	25							X		X		
Coelorinchus chilensis	TM	3	22				X	X		X		X		
Coelorinchus fasciatus	TM	6	31				X	X		X		X		X
Coelorinchus kishinouyei	OO	12	12-36			X		X				X		
Coelorinchus jordani	TM	2	27					X				X		
Coelorinchus jordani	OO	4	16-25			X						X		
Coelorinchus innotabilis	TM	3	28							X		X		X

Species	ref	no	size	fish	ceph	euph	cop	dec	mys	amph	per	poly	ech	mol
Coelorinchus japonicus	00	5	65			X		X			X		X	
Coelorinchus tokiensis	00	5	36-55			X		X					X	
Coelorinchus anatirostris	00	16	17-43	X		X							X	
Coelorinchus occa	TM	3	50							X			X	
Coelorinchus occa	MI	3	42	X			X	X						
Coelorinchus longissimus	00	4	20-35			X							X	
Trachyrinchus helolepis	TM	3	38										X	
Trachyrinchus trachyrinchus	TM	1											X	X

Most of the macrourids listed in Table 1 have food items from primarily one or two of the categories, and a few species contain items from all categories.

Several species had mostly pelagic prey in their stomachs. They include species of the relatively unspecialized subfamily Bathygadinae. Odontomacrurus murrayi, reported to be bathypelagic (Marshall, 1964) also had only pelagic prey. Malacocephalus laevis, Trachonurus villosus and Hymenocephalus species had food items primarily of pelagic origin; these species are characterized by large mouths, laterally compressed heads and relatively non-protrusible premaxillae.

Other macrourids that contained pelagic prey include Coryphaenoides rupestris, Coryphaenoides acrolepis, Coryphaenoides pectoralis and large specimens of Coryphaenoides filifer. All are large species found at moderate depths (1000 to 2000 meters).

Species that feed primarily on epibenthic prey are Lepidorhynchus denticulatus, Malacocephalus occidentalis, Coryphaenoides leptolepis, Macrourus berglax and Coelorinchus coelorinchus carminatus. The first two of these resemble each other in having moderately large, terminal mouths with large teeth. Both live at fairly shallow depths on the continental slope. Coryphaenoides leptolepis lives at depths below 2000 meters and is smaller than most other macrourids at that depth. It everts its stomach less frequently than

other species from the same depth, and its smaller swimbladder may be an indication that it is restricted to staying near the bottom (Pearcy and Ambler, 1974). Macrourus berglax lives over rocky bottoms on the continental slope. It reaches a length of at least one meter, has a highly protrusible upper jaw and benthic animals are found in small specimens.

Most species of Coelorinchus have food of benthic origin in their stomachs. C.c. carminatus differs from its congeners in having euphausiids and the three specimens of C. occa reported by Marshall and Iwamoto (1974) have fish and pelagic crustaceans in their stomachs. It is possible that these pelagic prey organisms come into contact with the bottom during their daily migration and are sometimes locally available as food.

Food organisms of benthic origin were found in the stomachs of two species of Mataeocephalus, two Trachyrincus species, most Coelorinchus species, Echinomacrurus mollis and Coryphaenoides carapinus. The first three genera are similar in having long rostrums and inferior mouths; most of them live at depths of less than 1000 meters. Echinomacrurus mollis has been caught only at depths greater than 5000 meters (Nybelin, 1957). Its head is spherical, inflated with large lateral line canals, and the mouth is small, inferior and highly protrusible. Coryphaenoides carapinus is a small species living at depths of 1600-2600 meters.

The only species with food from all three categories is Coryphaenoides armatus. Food of small specimens is mostly benthic and

those of large specimens are more of pelagic nature. It appears to be very generalized in its feeding habits when large, suggesting a scavenging feeding strategy (Pearcy and Ambler, 1974) or ascending into midwaters to feed (Haedrich and Henderson, 1974). Coryphaenoides armatus is the only species in which a fragment of an animal too large for it to swallow whole has been found. This is the only direct evidence from stomach contents that large pieces of detritus serve as food for macrourids.

The parasite fauna of some macrourids consists of a specific assemblage for each species with little overlap between species (Michael Moser (protozoans) and Ronald Campbell (helminths and others), personal communications). The intermediate hosts for parasites are not known in all cases, but the probable hosts are in the same general categories as the food that has been found in stomachs. The lack of overlap of parasite fauna suggests that there is some partitioning of resources between sympatric species.

Most macrourids feed on animals that they swallow whole. Those with longer rostrums and smaller mouths have more food of benthic origin than those with larger mouths, as noted by Okamura (1970b). The proportion of benthic prey is greater in shallower, smaller species and individuals within a species. Availability of food, as well as the morphology of the head, is an important factor in feeding habits.

## DISCUSSION

The differences in the morphology within the macrourids, and particularly the evolutionary trends that have led to the highly specialized head morphology of a long rostrum and small protrusible mouth, can be explained as a response to the availability of food in their environment. The architecture of the rostrum, protrusibility of the upper jaw and amount of lateral expansion of the oral cavity are the result of the interdependency of numerous anatomical differences which are integrated into adaptations for the utilization of different types of food. Adaptations for benthic feeding include a number of differences in the functioning of the head, particularly in relation to the creation of suction.

### I. Availability of Food

There are several potential sources of food for animals that swim just above the sediment surface in the deep sea. There are small animals that dwell within the sediment or on top of it, others that swim over the bottom, and large pieces of detritus such as the carcasses of midwater animals that may serve as food for bottom fishes. Also, it is possible for animals capable of hovering just off the bottom to adjust their buoyancy in order to ascend into midwaters to feed. The amount of potential prey in any of these

habitats decreases with depth and distance from land, as does the average size of the potential prey organisms (Rowe, Polloni and Horner, 1974). At a single depth the amount of possible food in any one category may be too little to support the predators that live there so that fishes may feed on a variety of prey. Benthic biomass estimates for the continental slope off New England show that the biomass of the infaunal animals to be of the same order of magnitude as that of the megafauna (including fishes, Rowe, Polloni and Horner, 1974). This suggests that the productivity of the benthos is not great enough to provide all of the food for the megafauna. The tiny animals of the abyssal benthos do not appear to be sufficient food for the large, mobile fish known from the same environment (Dayton and Hessler, 1972; Hessler and Jumars, 1974).

There are some sources of food on the sea floor that rarely appear in the stomachs of macrourids. The shells of bivalves and gastropods occur in macrourid stomach infrequently, while they have been found in rays, skates, zoarcids and other fishes. The crushing pharyngeal teeth of skates and rays and the benthic habits of zoarcids make hard-shelled benthic molluscs more available as food to them than for macrourids.

Prey organisms living near the bottom serve as food for fishes only if they are found and captured. Feeding on small, burrowing animals requires being able to locate them

under the sediment. That predation on burrowing animals is limited by the ability of predators to locate them is suggested by the observation that fishes are attracted to physical disturbances that scrape the top layer of sediment and expose the animals within (Caddy, 1973; Hessler, in preparation). This may be evidence that the fish are attracted to a source of food which is always present but inaccessible.

Feeding on actively swimming prey requires the ability to swim rapidly and overtake them or to trap them. Relying on large pieces of detritus for food requires that the fish be able to wait for long periods of time with no food, and then be able to swim long distances when something edible reaches the sea floor (Isaacs and Schwartzlose, 1975).

There is a reflection of the response to the availability of food in the deep sea in the life histories of some species of macrourids. Coryphaenoides armatus, one of the best studied macrourids, is found at depths of 2000 meters when small and at depths greater than 4000 meters when large. Small specimens have primarily food of benthic origin in their stomachs, while large ones have all sorts of prey items. The only reported fragment of an animal larger than the fish, a piece of a squid that must have been larger than the animal it was found in, came from Coryphaenoides armatus (Pearcy and Ambler, 1974). The food supply that this species seems to utilize when it is small is fairly constant and consists of small organisms that can be found in a limited

area of the bottom. The food supply of the larger fish may come at irregular intervals and be very abundant for short periods of time. The fish may spend long periods of time with little activity and swim long distances when attracted to large pieces of food.

Some of the highly specialized species of macrourids also show the same trend of living shallower when small, and then going deeper and feeding on larger and more active prey as they grow larger.

The most specialized macrourids in terms of the extremes of morphology are those with long rostrums. Mataeocephalus, Coelorinchus and Trachyrinchus are very different from each other osteologically and their similarities in rostrum shape and jaws appear to have arisen independently from one another. There are differences in the architecture of the rostrum which may indicate differences in the effectiveness with which they feed on benthic animals, and the extent to which it is used as a mechanical probe or as a sensing organ. The osteological support of the rostrum varies within Coelorinchus and between the three genera. The depth to which the rostrum may be used as a probe and the type of sediments that it may be used on will depend on its strength.

The evolutionary trends in the tribe Malacocephalini, including the genera Malacocephalus, Nezumia, Ventrifossa and Lucigadus, have been described by Iwamoto (1972). From an unspecialized ancestor there developed two lines, one, typified

by some species of Nezumia, led to a "mud-grubbing" habit, while the other led to off-bottom, active predators like Malacocephalus occidentalis. The feeding habits of the unspecialized ancestor are not discussed, and perhaps included food of several types. Most of the fishes in the tribe live commonly at depths of less than 1000 meters, and there is potential food to support large populations of fishes both in the bottom, if it is searched for, and swimming near the bottom, if it is chased after.

There are two major types of macrourids that feed primarily on pelagic prey. The first is the unspecialized primitive members of the group, Macruronus, Steindachneria, Bathygadus, Gadomus and Lepidorhynchus, all of which live at quite shallow depths. They resemble the shallow-living, active predators of the other gadiform families not only in their depth distribution but also in having large, terminal mouths and laterally compressed heads.

The other group of macrourids that prey on pelagic animals includes Coryphaenoides rupestris, Coryphaenoides acrolepis and Coryphaenoides pectoralis. They are large and moderately deep living. The poorly ossified skeletons of C. rupestris and C. pectoralis, and the occasional pelagic capture of these species (Iwamoto and Stein, 1974; Haedrich, 1974) attest to the strong possibility that they capture their food while well off the bottom, though they are frequently caught on the bottom. The nasals of C. rupestris have a narrow anterior medial

process, not apparent externally because of the huge lateral line canals that make the head appear inflated. Perhaps the shape of the nasals is a remainder from an ancestry as a benthic feeder, since they are similar in shape to those of Coryphaenoides carapinus, which feeds on small benthic animals, or it may serve a function that has not been discovered here.

The three pelagic feeding species of Coryphaenoides live at greater depths than the primitive pelagic feeders. Perhaps they have become pelagic predators because small benthic animals and large pieces of detritus were not quite enough to support such large fish, and productive midwaters could be reached with little effort, particularly when buoyancy was increased through lack of ossification.

## II. Predator Strategy and Morphological Adaptations for Creating Suction

Many predaceous fishes create a change in pressure as they open their mouths so that suction is used to draw prey into the mouth. Suction may be created through the rapid opening of the mouth and lateral expansion of the oral cavity (Lauder, 1976) or by rapidly swimming to the prey with the mouth open and using the swimming velocity to create a change in pressure (Nyberg, 1971). The protrusibility of the upper jaw has been said to increase the amount of suction in some fishes (Alexander, 1967a). A small opening, circular rather than notched around the edge, has also been found to be

important in maximizing suction (Lauder, 1976).

It is difficult to discuss the importance of suction in feeding when only dead specimens are available for study. There are enough differences in the factors important in creating suction within the Macrouridae, however, to merit some speculation on the means of creating suction and its importance in predator strategy.

In the "active predator" species, there is a large mouth, the oral cavity expands very far and cranial lifting is important in the opening of the mouth (figure 96A). Since the prey of these fishes consists of swimming animals, they probably capture them by swimming rapidly to the prey with the mouth wide open, and create suction in the same way as the bass (Nyberg, 1971). At the opposite extreme are those with small, highly protrusible mouths, a smaller amount of lateral expansion and long rostrums. If these animals search for prey on the sediment surface, they will not approach prey with much speed and suction, if it is created, occurs as a result of opening the mouth rather than swimming speed. The small, tube like mouth of Coelorinchus and Mataeocephalus will create more suction on opening than a large mouth. These fishes may feed by sticking their rostrum in the mud until they detect prey, then throwing up the sediment dorsal to the rostrum and picking out the animals.

## SUMMARY

Relations between feeding habits, size, depth range, mouth size, protrusibility as measured by length of the ascending process of the premaxilla and rostrum length are summarized in Table 2. Species examined are arranged in groups by their major food source-pelagic, epibenthic or benthic. Pelagic feeders are either shallow, large-mouthed, and without a rostrum, or large, moderately deep and with a small to moderate rostrum. Epibenthic predators are moderate to large with moderate mouths and moderate to very protrusible upper jaws. They do not show any correlation with depth or rostrum length. Benthic feeders are small and shallow, the majority of them having small, highly protrusible mouths and moderate to long rostrums.

Anatomical specializations for benthic feeding include: 1) elongate nasals meeting along the midline, supporting the rostrum, 2) protrusible premaxillae that fit into an internal socket in the cranium formed by the nasals and lacrimals, 3) lacrimal and infraorbital bones that form a strong ridge continuous with the preopercular shelf, 4) strongly scaled ridges of the head, 5) insertion of the adductor mandibulae 1  $\alpha$  on a high process of the maxilla so that its contraction is important in the protrusion of the premaxilla.

Long rostrums may be used as mechanical probes of the sediment. Protrusibility is probably important in creating suction in fishes that do not actively pursue prey.

Table 2. Summary of the feeding habits of the species examined in relation to size, depth of occurrence, mouth size, length of the premaxilla and rostrum length.

S--small M--moderate L--long (large)

Depth 1--less than 1000 meters 2--between 1000 and 2000 meters 3--more than 2000 meters

Species	Size	Depth	Mouth	Premax	Rostrum
<u>Pelagic</u>					
Macruronus novaezelandiae	S	1	L	S	-
Steindachneria argentea	S	1	L	S	-
Bathygadus macrops	M	1	L	S	-
Lepidorhynchus denticulatus	M	1	L	M	S
Coryphaenoides rupestris	L	2	M	M	M
Coryphaenoides acrolepis	L	2	M	M	M
Coryphaenoides pectoralis	L	2	L	S	S
<u>Epibenthic</u>					
Malacocephalus occidentalis	M	1	M	M	S
Coryphaenoides leptolepis	M	3	M	M	S
Macrourus berglax	L	1	M	L	M
Abyssicola macrochir	M	2	M	L	L
Coelorinchus longissimus	M	1	M	L	L
Coelorinchus occa	M	2	S	L	L

Species	Size	Depth	Mouth	Premax	Rostrum
<u>Benthic</u>					
Nezumia bairdii	S	1	S	L	M
Mataeocephalus acipenserinus	S	1	S	L	L
Coelorinchus coelorinchus carminatus	S	1	S	L	M
Coelorinchus chilensis	S	1	S	L	M
Coryphaenoides carapinus	S	1	S	L	M
Coelorinchus jordani	S	1	S	L	M
Coelorinchus innotabilis	S	1	S	L	L
Coelorinchus japonicus	M	1	M	L	L
Trachyrincus helolepis	M	1	M	M	L

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